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STUDIES ON REDUCTION IN PLANTS.[1]

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(WITH PLATES I–VI).

I. REDUCING DIVISION IN *ARISÆMA TRIPHYLLUM* BY RING- AND TETRAD-FORMATION DURING SPOROGENESIS.

IN connection with some studies carried on under my direction upon the embryology of certain of the Araceæ, an effort was made to investigate carefully the nuclear figures during the formation of the pollen from the mother cells of the archesporium. In *Arisæma triphyllum* the figures accompanying the heterotypic divisions are of such interest that it seems desirable to offer the results of the study as a contribution to our knowledge of this subject. Especially is this so because the evolution of the heterotypic figures is so divergent from that described for most of the plants heretofore studied; and in one phase coincides so plainly with certain of the types found in animals; while in another phase it departs, so far as I have yet been able to determine, from any type heretofore described.

Early in July the young leaves and the spadix of Arisæma, which are to appear the following spring, are formed, though quite small. They may be found by breaking the aerial shoot from the corm and removing several enveloping fleshy bud scales which protect the next season's leafy shoot. The stamens and pistils appear at this time as very minute protuberances on the

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surface of the spadix. During the latter part of July and early in August these become more prominent and begin to take on the character of stamens or pistils, as the case may be. The staminate plants can usually be determined during August and in September by the dried remnant of the staminate flower, which in many instances remains attached during the season; or by the cleft in the petiole of the leaf where it emerged. The pistillate plants can usually be determined by the presence of the forming fruit, though some of the smaller pistillate plants of one season become staminate for the next season, because of exhaustion in seed bearing. The archesporium of the staminate plants develops during July, August, and early September; or it may be mature by September.

The material for this study was collected and prepared by myself during September 1897. The staminate plants were brought to the laboratory and the material was fixed on the day of collection. The spadix was first removed from the bud so that the anthers were entirely exposed. One or two anthers from each spadix were removed and crushed on a glass slip in a drop of water for examination under the microscope to determine the stage of development. In this way all material where the pollen was already developed could be discarded, and only that preserved which was in one or another stage of mitosis. This made it possible to obtain good sections for study on a large number of the slides prepared. The nuclear figures can be quite readily seen in the living condition, but if there was any difficulty in determining the stage of mitosis, a drop of a solution of chloral hydrate was added, as suggested by Humphrey. The spores are formed centrifugally on the spadix, *i. e.*, the stamens at the base of the spadix are usually more advanced than those toward the apex, so that if the pollen was just formed in the lower stamens, the upper ones might show pollen mother cells in one or another of the stages of division. There was, however, considerable variation in the same stamen in this respect, while in a single locule there was little if any variation.

The material selected in this way was placed without further

preparation in Flemming's chrom-osmium-acetic solution for twenty-four hours. It was then washed in running water from twelve to twenty-four hours, dehydrated with grades of alcohol; decolorized by placing for twenty-four hours in bulk in hydrogen peroxid and alcohol, made by using 70 parts of a 95 per cent. alcohol and 30 parts of hydrogen peroxid. It was then stored in 75 per cent. alcohol after one rinsing. Six months later a portion of the material was placed in the hands of a student (Miss Susie P. Nichols) for study, and three months later the remainder was prepared on the slide for study by Mrs. W. A. Murrill under my direction. It was imbedded in paraffin, cut with a Minot-Zimmermann microtome 6.6–13.3 μ thick, stained, some in Flemming's triple safranin-gentian-violet-orange stain, and some with iron hæmatoxylin. For the present description of the material, and for the conclusions presented, the writer alone is responsible.

During the formation of the spirem the linin network gradually disappears, and a more or less continuous thread is formed. A distinct spirem was not observed, though this phase of mitosis has not yet been sufficiently studied. Even at the time of the longitudinal cleavage of the thread it was seen to anastomose more or less, where, in its windings, portions came in contact. At this time it presents the appearance of a very open, irregular network. The chromatin granules, at first distributed over the linin network, gradually accumulate in small masses scattered along the thread. As the spirem thread becomes more distinct it shortens, and accompanying this the small masses of chromatin increase in size, giving an appearance of a string of beads, or they present an irregular moniliform appearance. In addition to this beaded appearance of the thread the masses of chromatin are more or less irregular or angular. At some of the angles of the chromatin masses short delicate threads are attached, probably remnants of the linin reticulum which do not participate in the formation of the spirem. This, with the angularities of the chromatin masses, gives a somewhat ragged contour to the spirem. Quite early in the formation of the spirem, and before

the reticulum has completely disappeared, the thread shows a longitudinal splitting which is evident between the chromatin masses. In the early stages of the longitudinal splitting of the thread I have not seen the small chromatin masses divided. Each chromatin mass often appears to be made up of two smaller ones lying side by side, which have fused at the points of contact. Even in larger chromatin masses, and among the chromosomes in Arisæma, there is a strong tendency for those lying in contact to fuse more or less, so that the individuals of a single mass or of the chromosomes are often more or less obscured.

While the chromatin masses on the spirem are more or less fused, they are small and emarginate at opposite ends, and at a point coincident with the axis of the band. By this character one can distinguish the double nature, or paired condition of the masses. It suggests a division of the original masses, or the deposition of the chromatin in paired masses along the thread, which fuse more or less at the point of contact. These chromatin masses often stain unevenly, two portions separated by the axis of the thread or band taking on a deeper stain. The darker points lie in pairs along the thread, each separated by a paler chromatin area which runs for a short distance on either side along the division of the thread. At the point between the deeper staining masses the paler zones fuse.

As the spirem shortens, these paired chromatin masses are brought nearer together. Fusion among them takes place, so that the masses increase in length and breadth as the spirem broadens. The longitudinal division of the spirem is marked here and there, sometimes at quite regular intervals, by rounded, elliptical, or oblong openings in the chromatin, while in other places, for considerable distances, no line of division can be ascertained, though often the difference in the intensity of the stain marks the separation of the masses into pairs, while the paler surrounding zones are fused. As the band shortens, the contour becomes more irregular, showing crenations and irregularities, to which are often attached delicate strands, perhaps portions of the linin reticulum.

The chromosomes are marked off by the band separating into sixteen segments. So far as could be determined, this number is quite constant. The segments are not formed by an abrupt division of the spirem, but it appears as if the chromatin masses by shortening unite themselves into elongated areas, which are connected for a time by two delicate threads representing the original line of longitudinal division. The chromosomes lie around the periphery of the nuclear cavity and are quite variable in form; this is due to variations in the extent to which longitudinal fission has proceeded. In a few, longitudinal fission is complete, and a pair of long knotted rods is present. In others, there is a slight connection at one end or near the middle by the fusion of adjacent chromatin. In others, one or both ends of the flattened chromosome are indented or forked; in the latter case figures approaching the letters Y or X are formed. In many of the chromosomes the line of fission is shown by one or two small rounded openings or narrow open slits near the middle or near the ends; or the opening is long and extends from end to end, individuals of the pair being connected only at the end, thus resembling long irregular chain links. Some of the individuals of the pair lie parallel; others are separated more or less at the middle, when quite well defined rifts are formed. Still others resemble chain links twisted half way around, thus presenting a figure 8 appearance (*fig. 6*).

The length of the chromosomes is now from one third to one half or more the diameter of the nuclear cavity, and they show the irregularities presented by the spirem band, being knotted or angular along the edges or at the end. Delicate linin threads are often still attached at the knotted or angular enlargements.

The chromosomes now shorten, the chromatin becoming massed together, until their length is from one sixth to one fourth the diameter of the nuclear cavity. A larger proportion of them have now opened out in the middle in the form of rings, and, while they have shortened in length, their breadth is about the same as formerly, or they may be a little broader. This gives a more perfect ring form, but the chromosome is still somewhat longer than its

breadth, so that the line of longitudinal fission can be determined. The line of longitudinal fission is also indicated in other ways. Other chromosomes at this time are present in the form of short plates, some of which show slight indentations at the end, while in others longitudinal fission is complete, and a pair of rods is formed.

During the process of shortening of the chromosomes, the greater part of the chromatin usually becomes massed at four definite points in the ring, or plates, or pair of rods. These denser masses of chromatin lie near the ends of the rods, or near the ends of each lengthened half of the ring or plate, and are connected by paler staining areas, the density of which varies in different rings. These four masses of chromatin, in the ring or in the rods as the case may be, form the tetrad. These rings and tetrads in *Arisæma triphyllum* are very distinct, as much so as in certain animals. The two lengthened halves of the rings are usually more nearly separated along the line of longitudinal fission than along the line of transverse division, so that they quite readily separate. Each half of the ring is more or less crescent shaped, and the ends, instead of being rounded, are often quite regularly angular, presenting figures that frequently aid one in determining the orientation of the cleavage line. Up to this time the chromosomes still occupy their position around the periphery of the nuclear cavity, and, up to quite a late period, often show fragments of linin attached.

The nuclear membrane now disappears, and the kinoplasmic threads, which are to form the spindle, enter and move the chromosomes up to the nuclear plate. The threads first radiate irregularly in all directions, but converge more and more at two poles as they gradually form the spindle. As this takes place, there seem to be two centers of force which lie at the poles of the spindle, and occasionally this is manifested a short time before the spindle is complete by radiations of kinoplasm about the poles in the form of rays, which suggests a centrosphere figure (*fig. 14*). This was observed very plainly in one case, and perhaps similar figures in other plants have led observers to interpret them as centrospheres.

As the chromosomes are drawn to the nuclear plate they lie in various positions. At first it was thought that the axis of the chromosome, whether a ring, a pair of rods, or plate, lay perpendicular to the axis of the spindle. I have observed them in this position a short time before the spindle is complete. In some such cases, the position of the spindle threads suggests that the chromosomes are pulled around before division so that the axis is parallel with the spindle axis. In other preparations, the chromosomes, where they lie close together, tend to fuse to such an extent that it is impossible to determine in what position they lie at the nuclear plate, *i. e.*, whether parallel with or perpendicular to the axis. In a large number of preparations conditions are such as to lead me to believe that the axis of the chromosome is parallel with the axis of the spindle. The chromosomes are so numerous and of such size that they cannot all lie at the periphery of the plate, but occupy the center of the nuclear plate as well, so that an end view of the nuclear plate shows the chromosomes quite evenly distributed over this area. In many cases a large number of them are fused, and curious figures are thus presented. At other times they lie entirely separated, so that the individual rings, or pairs of rods, can be seen and counted in an end view of the nuclear plate. Where the section is cut so as to show an oblique view of the plate, the groups of tetrads, or pairs of rods, can be well seen and counted. From studies of sections in this direction, it appears that there are sixteen groups of tetrads, which would make sixty-four individual chromosomes, thirty-two to be distributed to each daughter nucleus of the first division, and perhaps sixteen to each daughter nucleus of the second division. A side view of the spindles of such preparations, at the nuclear plate stage, shows the long axis of the rings or pairs of rods to be parallel with the axis of the spindle. Since the chromosomes are distributed through the center of the nuclear plate as well, they lie like a bundle of chain links. The form of the ring, as suggested above, indicates that the axis of the longitudinal cleavage of the spirem or of the tetrad lies parallel with the axis of the spindle.

This is important in determining the character of the first division, as to whether it is to be a longitudinal or a transverse division of the chromosomes.

Not only does the form of the ring aid in determining the position of the chromosomes at the nuclear plate stage of the first division; the paired rods also serve to determine this. These lie parallel with the axis of the spindle. Even before the rings have moved to the nuclear plate there is a great tendency for them to separate into longitudinal halves. This occurs also at the nuclear plate stage. The tetrads separate more readily along the line of longitudinal division than they do on the line of transverse division. For this reason, at the nuclear plate stage, the figures with paired rods, rings partly or completely separated along the line of the lengthwise cleavage of the spirem, together with the form of the rings, should determine the position of the long axis of the chromosomes. The tufts of spindle fibers are attached to each individual of the tetrads, and transverse or reducing division of the chromosome results as these are drawn away from the nuclear plate. In many cases the sixty-four tetrads, thirty-two to each pole, move as distinct individuals, so that longitudinal, as well as transverse division, occurs in the first mitosis of the mother cell nucleus. But while transverse division occurs during the first mitosis of the nucleus, longitudinal division of the chromosome takes place first. The peculiarity of Arisæma, then, is that, while longitudinal division precedes transverse division of the chromosome, both divisions occur during the first or heterotypic division, and the real reduction follows soon the pseudo-reduction in the heterotypic division.

The only other account of a reducing division in the first mitosis which I have noticed is that by Korschelt in the study of the development of the egg of the annelid Orphryotrocha, quoted by Wilson in "The cell in development and inheritance," p. 201. During the first mitosis in oogenesis, the spirem segments into four chromosomes, which is the normal number in the somatic cells. These split, and then the pairs fuse

together again, the four chromosomes arranging themselves in a tetrad, two going to the first polar body and two remaining in the egg cell. These two split and form another tetrad, two chromosomes going to the second polar body and two remaining in the egg nucleus. This brings about reduction in the first mitosis.

Beliaieff[2] for a number of years has maintained that a reducing division takes place in plants, and, based on his studies of the division of the pollen mother cells of Iris, classifies the modes of division of the nucleus in plants into three types: (1) the vegetative division; (2) the heterotypic division; and (3) the reducing division. The heterotypic division takes place, as is well known, in the first mitosis of the pollen mother cell, and the reducing division accompanies the second mitosis.

Calkins[3] announces reducing division during the second mitosis of the pollen mother cell in Pteris and Adiantum. Calkins was unable to determine whether the reducing division in Pteris and Adiantum occurred during the primary or secondary mitosis, since the tetrads were packed so closely in the nuclear plate of the first division. During the secondary mitosis the diads elongate to form a rod. This elongation he thinks takes place in the direction of the axis of the spirem, and would thus show that the primary mitosis is an equation division, while reduction takes place during the secondary mitosis. Nevertheless he recognizes that it is immaterial whether reduction takes place during the first or second division. The formation of tetrads in the prophase of the primary mitosis is generally regarded as the preparation of the number of the chromosomes which are to be eventually distributed to the four daughter nuclei of the second mitosis; and where the tetrads are formed by one longitudinal and one transverse division of the segment of the spirem, it is equivalent to reduction in the prophase of the first division,

[2] BELIAIEFF, W.: Ueber die Reductionstheilung des Pflanzenkernes (Vorläufige Mittheilung). Ber. d. deutsch. bot. Gesells. **16**: 27–34. 1898.

[3] Chromatin reduction and tetrad formation in pteridophytes. Contrib. Dept. Bot. Columbia Univ. **5**: 101–115. *pl. 295, 296.* 1897.

though usually, so far as accounts go, the final separation for the reduction does not occur until the second division. In Arisæma the mode of tetrad formation by longitudinal and transverse division is such as to effect reduction in the prophase of the first division, while during metaphase and anaphase the reduction is completed by the separation of the tetrad of the transversely divided diad.

II. REDUCING DIVISION OF THE CHROMOSOMES IN *TRILLIUM GRANDIFLORUM* DURING SPOROGENESIS.

In studying the development of the pollen of *Trillium grandiflorum*, the chromosomes were found to be of such large size as to offer, possibly, a good opportunity for an investigation which might throw some light on certain of the problems of mitosis during sporogenesis. The preliminary studies were made upon material collected during the autumn and winter of 1896–7. With the experience of one season's work it was possible to plan for the collection of a quantity of material in different stages of development. The young flowers of Trillium begin their development in June and July of the previous year, and by autumn they are well formed, though they remain protected in the sheathing bud scales during the winter. So far as I have found, the archesporium is completed and the period of growth of the pollen mother cells is closed with the oncoming of winter, if not before. The period during which the division of the pollen mother cells takes place extends over seven or eight months. This is due not only to some variation in the time of maturing of different plants in different localities, but also to temperature. In the open woods, on rather high ground, where the plants are protected from cold north and west winds and are exposed to the warmth of the sun, the pollen is often mature in the latter part of September. In the cool ravines and open places exposed to north winds, the pollen is formed in warm days during February, March, or April, according to the season, and to some extent also according to the state of maturation in different individuals.

Very cold weather checks the progress of mitosis, but when

the mother cells have reached the proper state of maturation a few warm days in the winter or early spring months are sufficient for the two successive divisions. It appears that during the winter season, when the nights are cool and the days warm, the mitotic figures may be prolonged for several days. For this reason it is not difficult to prepare a large quantity of material in different stages of division. For the present study the material was collected during the month of February 1898. Some of this was growing in a garden where it was transplanted the year before, while the bulk of the material was collected from wooded ravines, from one to two miles distant from the laboratory, the plants being easily found by raking off the leaf covering on the ground.

All the material was examined before fixing in order to know just the stage of division in individual plants, and even assorted into lots showing the spirem stage, first and second division, for convenience in cutting material of any desired stage. During division the chromosomes are so large and the cytoplasm so clear, one can easily determine the different stages with a one sixth objective, so that desired material could be assorted into that showing prophase, nuclear plate, anaphase, etc. In each individual flower, the tip of one of the stamens was removed, crushed in a drop of water on the slide, and examined first with a two thirds objective, then with a one sixth. In this way undesirable material could be rejected.

Before placing in the Flemming solution, sometimes the tips of all the anthers were cut off, while other material was placed in the fixing solution with the anthers closed. After the removal of the sepals, petals, and the apex of the pistil, so that the fixing solution could enter the locules of the young carpels, the entire androecium still attached to the receptacle was thrown into the solution. This made it possible to section several anthers of an individual flower together.

The fixing solution used was Flemming's chrom-osmium-acetic solution. The material remained in this from fifteen to twenty-four hours, was washed from twelve to twenty hours in cold

running water, dehydrated in grades of alcohol to 95 per cent., then decolorized in mass in alcohol of 70 per cent. which was diluted with hydrogen peroxid. It was then passed back to alcohol of commercial strength, then through absolute alcohol, and cedar oil; finally it was infiltrated with paraffin and imbedded. It was then stored in the paraffin blocks for a few weeks or months as time became available for cutting and staining. The material was cut on a Minot-Zimmermann microtome and stained, some with the triple stain (safranin-gentian-violet-orange) and some with iron-hæmatoxylin.

The early stages of the spirem have not yet been studied, but the spirem forms a broad and probably continuous band. Before it segments, it often shows a differentiation, where not overstained, into a ground substance giving a pale purple or pale violet reaction with the gentian violet, and more deeply stained bodies which are in pairs and appear at quite regular intervals in the band. The line of separation which runs along between the pairs of denser chromatin masses marks the line of longitudinal division of the spirem, though the ground substance often shows no division line. As the spirem matures, here and there are seen short openings along the middle line. This is especially well marked as the spirem segments into the chromosomes. The individual chromosomes often show traces of longitudinal division, by short openings near one end, or at the middle, oftener at the ends, where there is a slight indentation; or, the division proceeding deeper, the end is more or less forked, resulting in Y- or U-shaped figures.

The spirem segments into about six chromosomes. They are at first rather long and become somewhat shorter and broader as they move to the nuclear plate of the spindle.

At this time the usual changes in the nucleus take place. The membrane disappears and the threads of kinoplasm move in, showing first a radiating arrangement and gradually moving to converge into the two poles as the spindle is formed; the chromosomes are drawn toward the center and are finally oriented in the nuclear plate. The chromosomes are broad, flattened,

and irregularly oblong. There is considerable variation in size.

They are very characteristic in form and structure. A few show narrow slit-like openings in the middle. A few of this form become very short and the opening then is somewhat rounded, so that a ring form is the result. This is comparatively rare. Others are divided at the ends, some showing a slight emargination, while some are more or less deeply forked, showing a tendency to form X and Y figures. Combinations of these two types are also found, so that there will be an opening in the middle, while the ends are somewhat forked, or one end is deeply divided. More characteristic, however, is the tendency to a differentiation in the density of the chromatin, which is especially marked when the chromatin is not stained too deeply. This differentiation of the chromatin is of the same kind as that manifested in the spirem and shows the paired condition of the chromosomes. The ground substance of the chromosome in these cases shows uniformly a paler tint and is translucent, while the denser masses of chromatin stain very dark and are more or less opaque. These chromatin masses are paired just as they are in the spirem, and probably result from the division of single chromatin masses in the early fission of the spirem. When these chromatin masses are well marked in the chromosomes, they seem to be uniformly of the same number so far as observed. There are often found well marked pairs of chromatin masses, each mass lying in the edge of the bar, four at the ends (two at each end) and four near the middle (two on each side near the middle), making eight in all.

Very frequently the edge of the bar is undulate, the prominences on the edges occurring at the location of the chromatin masses. The apparent uniformity in the number of these chromatin masses in the chromosomes is, perhaps, of considerable interest, and one is led to inquire whether they represent the units of the chromosomes or whether each one is a member of a tetrad group. If the latter is the true interpretation, then there would be in each chromosome of *Trillium grandiflorum* two united tetrads, or the chromosomes in the prophase of the

heterotypic division would be quadrivalent, instead of bivalent, as in the case of the normal tetrad.

As the chromosomes are drawn toward the nuclear plate, they become bent, so that each one represents a short arc of a circle or a broad open U form, as if drawn more forcibly by threads attached to the middle portion. As they are oriented on the nuclear plate transverse to the axis of the spindle they at first stand in various positions. Some lie tangentially, with the convex side toward the axis of the spindle and with both ends at the periphery, while others lie so that one end is directed toward the axis, with the other end at the periphery. In this way they are sometimes "convolute" or more or less "imbricate" in the nuclear plate, and may remain so for some time during the metaphase, or while separation at the nuclear plate is beginning to take place. Before separation has proceeded far, however, the chromosomes are usually more bent upon themselves, with the free ends of the U nearer together and directed outward in the usual way.

While the monaster is forming, and many of the chromosomes stand with one end directed toward the axis of the spindle and the other radiating therefrom, certain ones which are strongly lobed at the ends present a figure which leads one to think that the ends might be separated first, and that the chromosomes might then, in the anaphase, move to the poles in the form of a U, but with the concave or open side directed toward the poles, or that the inner ends might be separated first, and the chromosomes then move to the poles in the rod form. It does not seem, however, that the movement of the chromosomes has begun in such figures, and it is suggested that they are not yet drawn into proper position in the nuclear plate.

As separation of the paired chromosomes begins, the larger number of spindle threads appear to be attached in one tuft at the middle. The flattened U-shaped chromosome now broadens at the middle, in response to the tension of the tuft of threads attached at this point on either half, and the chromatin substance is soon drawn out into a short process on either side which

becomes the point of the V-shaped daughter chromosome, or forms a slight projection on the convex side of the U-shaped ones if this form is retained. No pull is exerted on the end of the chromosome, the ends of the pairs remain united, or in position at the periphery of the nuclear plate, while the middle portions are drawn toward the opposite poles, and in opening out thus, the dividing chromosome forms the diamond-shaped figure when seen from in front (*fig. 18*).

During the anaphase the chromosomes are V-shaped or U-shaped, and show considerable irregularity in contour, being more or less nodulose, often showing still the four dense chromatin masses. Some close up behind and form rings, some divide in front and form two rods. As the chromosomes approach the poles the polar ends converge, so that the chromosomes lie close together around the periphery of the ends of the spindle. Lying in this position the daughter nucleus is formed. The form of the daughter nucleus is somewhat like the half of a biconvex lens, the convexity being outward, while the truncated end lies toward the cell plate now formed by the connecting spindle threads. The form and position of the chromosomes give to the daughter nucleus its shape, for as the closed ends of the V- or U-shaped chromosomes converge at the apex of the cone, the spreading arms of the open end cause the nucleus to broaden out on the side facing the cell plate. The nuclear cavity now appears and the chromosomes are lying on its periphery against the nuclear membrane. They become usually more irregular in form, with angular points on the edge to which appear to be attached delicate threads connecting with the nuclear membrane, or reaching to an adjacent chromosome.

Where the nucleus is small by the close crowding of the large chromosomes, it is quite impossible to determine whether the chromosomes unite in such a way as to form a spirem. The nucleus does not, however, pass into a resting stage with the linin reticulum upon which the chromatin is distributed, but the chromatin bands remain intact. In the large nuclei, where the chromosomes do not lie so close together, they appear in most

cases to remain distinct, and in the form of V- or U-shaped bands, or often they are horseshoe-shaped, and sometimes form rings. In some cases it appears as if the arms of adjacent chromosomes coming in contact had fused at the end, but in no case could I see that they were thus united around the nucleus to form a continuous spirem, as described by Mottier for Podophyllum. Sometimes it appeared as if two had united by their ends to form a very large ring. In other cases the chromosomes may be permanently separated into two groups during this period.

As the nuclear cavity is formed and the first spindle is disappearing, the free ends of the chromosomes sometimes bend inward partly over the truncate side of the cavity, and at other times the chromosomes do not occupy the regular position which they usually show when they have reached the poles. In these cases ends of the chromosomes may be fused here and there, but in all stages several free ends are to be seen, and the figures presented by the nucleus are such as to lead one to believe that the chromosomes remain distinct through this phase. If the daughter nucleus is not elongated when first formed, it very soon begins to elongate in a plane parallel with the cell plates, so that it becomes nearly or quite twice as long as its diameter, and it is more or less inequilateral, the convex side being toward the periphery of the primary mother cell, while the plane side faces the cell plate. In opening out in this way the chromosomes become more and more distinct. The elongation of the daughter nucleus often takes place while the chromosomes are moving to the poles (*fig. 21*). In such cases the chromosomes are more easily followed, and the evidence is quite convincing in support of the view that the individuality of the chromosomes is preserved from the anaphase of the first division through to the prophase of the second mitosis. From the V- and U-shaped forms possessed by the chromosomes as they go to the poles, many of them change to horseshoe form, or some to complete rings by the free ends converging while the arms part slightly at the middle portion. In a number of cases the chromosomes divide

transversely at the convex end and the two rods lie side by side or near each other. The nuclear membrane now disappears and the kinoplasmic threads enter to form the spindle for the second division.

The elongation of the nucleus while the chromosomes are moving to the poles shows that the forces are in play which form the spindle for the second division. It is evident also that the chromosomes remain distinct, and that they are soon to be again separated transversely.

The elongated form of the nucleus marks the position of the spindle for the second division, and the poles of the spindle lie near the poles of the elongated nucleus. The spindle is therefore inequilateral, the poles being curved toward the cell plate of the first spindle figure. At the same time the chromosomes begin to move inward to the cell plate, and in doing so show the same general form which they possessed during the anaphase of the heterotypic division, which it seems they possess through the short period which intervenes before the formation of the second spindle figure.

During this time there is no longitudinal cleavage of the chromosomes. Even should the chromosomes form a continuous band in the daughter nucleus of the first division, there is no longitudinal splitting of the same at this time. Sometimes there is an appearance of a longitudinal fission of the chromosomes where the edges seem to be more deeply stained than a middle zone along the axis. This was found to be due, however, to the deeper staining of an outer layer of the large chromosome, and in properly stained preparations can be seen at any stage of mitosis.

If longitudinal fission of the chromosomes takes place during the second division, it would then be sought for in the nuclear plate stage.

Since the chromosomes during the prophase of the second mitosis are of the same general form as those of the anaphase of the first division, and very likely preserve their identity through the short intervening period, they should be chiefly V- or U-shaped. This is the case, as the examination of a large number

of preparations proves, while a few are ring form (*fig. 30*), and still others, having divided transversely at the apex of the V or the closed end of the U, exist as a pair of rods.

As the chromosomes approach the nuclear plate the arms of the V- or U-shaped ones close together, and, usually at the same time, transverse division takes place at the closed end. In this way all the chromosomes become of nearly uniform shape, consisting of two parallel or nearly parallel rods, which become more or less fused along the line of contact. The result of this is to form a double chromosome, very broad and irregularly oblong, which resembles in a striking manner the paired chromosomes at the nuclear plate of the first or heterotypic division, though they are formed as a result of folding and transverse division instead of by longitudinal cleavage. As the paired chromosomes are oriented on the nuclear plate, they usually become bent in such a way that the convex side lies toward the axis of the spindle, while the ends are directed outward, and the axis of the double chromosome is perpendicular to the axis of the spindle. The figure therefore presented by the metaphase of the second division is very much like that of the heterotypic division, and the only way in which one can determine that these belong to the second division is by the fact that there are two such spindles within the wall of the mother cell. Variations in their position in the monaster occur. One end of the chromosome may be directed inward toward the axis of the spindle, so that a few of them may be somewhat convolute; or the bent end may lie tangentially at the periphery of the spindle; or the chromosome may be nearly straight and standing on one end, while the other end radiates outward. As the position of the chromosome varies at the nuclear plate, so the figures presented during the anaphase vary, but the result is the same in each case.

The broad chromosomes lying thus at the nuclear plate, their edges face the poles of the spindle; the threads of the spindle which pull on the chromosomes are attached to that portion of the chromosome on either side which lies near the periphery of the spindle. On those which are bent so that both arms of the

U radiate equally, the threads are attached at the middle; on those which stand so that the arms radiate unequally the threads are attached somewhere between the end and the middle; while those which stand on the end have the threads attached at the end of each edge. The pull of the threads attached at the different points on the differently oriented pairs of chromosomes separate the individuals of the pair, the separation beginning at the point of attachment of the thread, and, as the portions are drawn toward the poles, the liberation proceeds until the members of the pair are no longer in contact. The different figures presented may be grouped all in three types, the V or U, the hook or the V with unequal arms, and the straight rods. These as can be readily seen are dependent on the point of attachment of the spindle threads.

The result of this separation of the individuals of the paired chromosomes in the second mitosis is a reducing division of the chromosomes, or a qualitative reduction of the chromatin substance; for, as we have seen, the paired chromosomes in the second mitosis are formed by the looping of longer chromosomes, which often open out at the bent end before reaching the nuclear plate. The second division results simply in the separation of the arms of this loop, and the distribution of each to a different daughter nucleus. It may be admitted here, then, with a feeling of reasonable confidence, that in *Trillium grandiflorum* a reducing division of the chromosomes, or in other words, a qualitative reduction of the chromatin takes place during the second division of the nucleus in the development of the pollen or microspores. One may well be cautioned against a hasty judgment in the interpretation of the figures presented during sporogenesis, because of what seems to be contradictory evidence given by different investigators upon the question as to whether or not a reducing division of the chromosomes takes place in plants, and it is only after careful study of an excellent series of preparations that I am led to present this as my conviction of the nature of the process as it occurs in Trillium. The large size and small number of the chromosomes, as well as

their form, have contributed in no small degree to the results obtained.

As is well known, the investigations of Mottier[4] upon division of the pollen mother cells in Podophyllum, led Strasburger[5] to believe that a reducing division of the chromosomes occurred during the second mitosis of the pollen mother cell. But more recent researches by Mottier, especially upon the condition of the chromosomes in the daughter nucleus and the origin of the chromosomes for the second division, led Strasburger[6] to recede from his former position and to reaffirm his conviction that the second division is the result of a longitudinal cleavage. According to Mottier, the chromosomes unite in the daughter nucleus of the first division in such a way as to form a continuous single band, *i. e.*, a band made of single chromosomes united end to end, the arms of the V-shaped chromosomes and of the paired ones, where transverse division has taken place, open out to join with the arms of neighboring ones. This band forms the spirem, which splits longitudinally before it segments into the chromosomes for the second division. As a result of this process of longitudinal fission of the spirem in Podophyllum, the segments or chromosomes are paired, but the pairs in the case of Podophyllum would then be the result of longitudinal fission, The separation of the members of the pair at the nuclear plate during the second mitosis would not then be here a reducing division.

These conclusions of Strasburger and Mottier led me to study very carefully the same stage in Trillium. As I have indicated above, the evidence seems to me to show that the chromosomes retain their individuality through the daughter nuclei from the anaphase of the first division to the prophase of

[4] MOTTIER, D. M.—Beiträge zur Kenntniss der Kerntheilung in den Pollen-mutterzellen einiger Dikotylen und Monokotylen. Jahrb. f. wiss. Bot. **30**: 169–204. *pl. 3–5*. 1897.

[5] STRASBURGER, E.—Ueber Cytoplasmastructuren, Kern- und Zelltheilung. Jahrb. f. wiss. Bot. **30**: 375–405. 1897.

[6] STRASBURGER, E. and MOTTIER, D. M.—Ueber den zweiten Theilungsschritt im Pollenmutterzellen. Ber. d. deutsch. bot. Gesells. **15**: 327–332. *pl. 15*. 1897.

the second. It might, however, be admitted that they unite to form a continuous spirem, without invalidating the conclusions reached in this study, for I have not found the slightest evidence of a longitudinal fission during the daughter nucleus stage. On the other hand the chromosomes, as the nucleus opens out, appear in the same form and number as shown at the close of the first division, that is, in the form of a letter V or U, or in rings, or even in the form of paired rods, which form more or less the same figure, and agree in this respect with the same types described by Beliaieff for the same stages.

The origin and form of the chromosomes in the first division of the pollen mother cell of Trillium, and the figures presented at the nuclear plate, show that the first division is heterotypic, though the transverse division of the chromosomes at this time, which indicates the tetrad character, is rarely present. The figures presented by the second division are exceedingly interesting, since they suggest the heterotypic division also, as is indicated by rings, in some cases, which are formed by the closing of the open ends of a V or U figure. There is thus a semblance of a heterotypic figure, with reducing or transverse division during the second mitosis in the sporogenesis of Trillium, and it would be interesting to know if the heterotypic figure described by Farmer[7] during the second mitosis in the sporogenesis of some liverworts, results in qualitative reduction. The figures presented by the chromosomes at the nuclear plate of the second division are strikingly similar to those which exist during the true heterotypic mitosis, and the separation of the chromosomes gives, during the anaphase, figures exactly like those shown during the first division.

A larger number of chromosomes in the second division, perhaps, are of the hooked form, and some are of the rod form, though both the hook and rod form are found rarely in the first division. It would appear that in Trillium, as well as in Arisæma, as shown by my studies on reducing division in that genus, the

[7] FARMER, J. B.—On spore formation and nuclear division in the Hepaticæ. Ann. Bot. 9:469–523. *pl. 16–18.* 1895.

form of the chromosomes and the mode of separation at the nuclear plate would not permit of classification into the types suggested by Beliaieff.[8] It is quite reasonable to believe that in mitosis, where the size and proportional dimensions of the chromosomes vary, as they are so well known to do, a great variety in the form of the chromosomes may exist, and that, correspondingly, there may be great variation in different species manifested in chromatin figures and evolutions, even where the same result is finally obtained.

In the peculiarities of the second mitosis of the pollen mother cell in *Trillium grandiflorum*, there is presented a distinct type in the evolutions of the chromosomes during the reducing division. Considerable interest attaches also to the peculiarity of the large chromosomes during the anaphase and metaphase of the first mitosis, where there is an appearance of eight denser portions of chromatin in the chromosomes, arranged in four pairs in such a way as to suggest two tetrad groups in a single segment of the spirem. In connection with this, it is interesting to note, that, while in *Trillium grandiflorum* during the first mitosis in the pollen mother cell there are only six chromosomes, in a number of the Liliaceæ there are twelve. This indicates, possibly, that the segments of the spirem in Trillium here represent four chromosomes, fused end to end (quadrivalent), instead of two (bivalent), which is usually the case as a result of the pseudo-reduction. *Arisæma triphyllum*, according to my studies on this species, also presents a distinct type, in that the reducing division, though following the longitudinal division, occurs during the first mitosis.

That there should be variations in the evolutions performed by the chromosomes in different plants, such as to represent different types, is what one might expect, not only in view of the great variations in the size and form of the chromosomes in different plants, representing different types of chromosomes, but also in view of the tendency to variation so manifest in many of

[8] BELIAIEFF, W.—Ueber die Reductionstheilung des Pflanzenkernes (Vorläufige Mittheilung). Ber. d. deutsch. bot. Gesells. **16**: 27–34. 1898.

the phenomena of plant life, extending even to nuclear phenomena, illustrated by the different types in fertilization, as shown by the investigations of Ikeno[9] in Cycas, Shaw[10] in Onoclea, and Blackman[11] in *Pinus sylvestris*, as well as by Miss Ferguson[12] in *Pinus Strobus*.

Is it not well to inquire if some of the divergent and contradictory results regarding the behavior of the chromosomes obtained by different investigators, when dealing with different plants, are not due to the fact that we are dealing with different types in some cases? Are there not among plants different types of chromatin reduction? So that in one type there is represented a mass reduction, or quantitative reduction of the chromatin; in another type a pseudo-reduction, or numerical reduction only of the chromosomes; and in another type a qualitative reduction of the chromatin or reducing division of the chromosomes? Touching the hereditary or constitutional influences of fertilization, we recognize different types in plants, as shown by close- and cross-fertilization; and different types also in the mechanism for bringing about pollination.

Some of the bewilderment which now surrounds certain phases of the study of the morphology of the nucleus will, I believe, disappear, if we recognize that there is such a thing as a reducing division or qualitative reduction in plants as represented by such types as Trillium, Arisæma, Adiantum, Pteris, Iris, etc.; that there are plants in which only a quantitative or numerical reduction occurs, represented by such a type as Podophyllum; and possibly that there is still another type, where

[9] IKENO, S.—Untersuchungen über die Entwickelung der Geschlechtsorgane und den Vorgang der Befruchtung bei *Cycas revoluta*. Jahrb. f. wiss. Bot. **32**: 557–602. *pl. 8–10*. 1898.

[10] SHAW, W. R.—The Fertilization of Onoclea. Ann. Bot. **12**: 261–285. *pl. 19*. 1898.

[11] BLACKMAN, V. H.—On the cytological features of fertilization and related phenomena in *Pinus sylvestris* L. Phil. Trans. Roy. Soc. B. **190**: 395–426. *pl. 12–14*. 1898.

[12] Miss Ferguson's studies were carried on under my direction in the Bot. Lab. Cornell University, and a paper, yet unpublished, was read before the Bot. Soc. Am. Aug. 1898, entitled "A preliminary note on fertilization in the white pine."

in the same plant qualitative reduction may take place in some cells, while quantitative or numerical reduction only takes place in others. This seems to me, as a working hypothesis, more reasonable than to insist, because one type has been found in one or several plants, that all plants must conform to it.

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EXPLANATION OF PLATES I–VI.

(All the figures are drawn to the same scale, using a Zeiss microscope, compensation ocular 12, and the 2^{mm} homogeneous immersion objective, the image being thrown down even with the base of the microscope. The figures are reproduced from these drawings without any reduction.)

PLATES I AND II. Arisæma triphyllum.

FIG. 1. Spirem stage of nucleus showing the dividing thread with chromatin masses on it. The masses of chromatin are partly divided, and appear as paired masses along the thread.

FIG. 2. Portions of partly formed spirem, showing indications of longitudinal division.

FIG. 3. Early stage of chromosomes, just after segmentation of spirem band, showing different stages of longitudinal division, forming oblong plates with ends slightly forked, or those approaching X and U forms, where the division is more marked. Fragments of linin are still attached.

FIGS. 4, 5, 6, 7. Different stages, showing the gradual shortening of the chromosomes in some cases, in others different forms of chromosomes, in same stage as those in *fig. 3*. In *figs. 4* and *5*, some are opening out to form rings; in *fig. 6* one of the oblong rings is twisted to form a figure 8, and in *fig. 7* one shows two openings along the line of longitudinal division. All of the chromosomes in these figures are yet more or less irregular, angular, and show fragments of the linin attached.

FIGS. 8, 9, 10. Chromosomes much shortened, and a large number of them in the ring form. In *fig. 8* two have completely divided to form rods, two form oblong plates with forked ends, and one forms a ring, while in *fig. 10* nearly all are in the ring form. Some of them are still angular, and show the peculiar form of so many of the rings of Arisæma. The tetrads are being formed by the accumulation of the chromatin in denser portions near the ends of the rods, and near the ends of each half of the rings, the paler zone across the middle showing the line of transverse division. Linin threads are still attached to some of the angles. The nuclear membrane is still intact, and the chromosomes are arranged around the periphery of the nuclear cavity in the positions occupied by them when they separated as segments from the spirem.

FIGS. 11, 12, 13. The nuclear membrane has disappeared, and threads of kinoplasm are entering to form the spindle; chromosomes in the form of rings, paired rods, or angular plates, which are solid or with a central perforation indicating the ring form.

FIG. 14. Spindle with chromosomes approaching the nuclear plate. The poles of the spindle show radiating lines of protoplasm indicating centers of force.

FIG. 15. Chromosomes in the nuclear plate stage, but they are in this preparation so fused that it is impossible to see the way in which division takes place.

FIGS. 16, 17. Chromosomes beginning to separate at the nuclear plate; rings, paired rods, and tetrads can be seen. The rings and paired rods are lying with the long axis parallel with the axis of the spindle, longitudinal division has taken place in some and is taking place in others, so that the halves of rings form crescent-shaped rods, the tetrads are indicated by deeper staining portions of the rods or rings.

FIGS. 18, 19. A little later condition of the same (metaphase) stage; longitudinal division has taken place so that nearly all the rods or halves of the rings have separated, and by the pulling of the spindle threads the tetrads are being drawn apart transversely to the axis of the chromosome, to bring about the reducing division.

FIGS. 20, 21. Polar view of the metaphase, showing that the chromosomes are distributed all through the nuclear plate. Sixteen groups can be counted, bearing in mind that a pair of rods, or a tetrad, makes a group. Some of the chromosomes are turned somewhat obliquely, especially in *fig. 20*, which was an oblique view of the plate, and in some cases the paired rods are seen only from the end.

FIG. 22. The tetrads have nearly separated by transverse division.

FIGS. 23, 24. Tetrads, about 32 on each side, approaching the poles during the anaphase of the first mitosis.

PLATES III–VI. Trillium grandiflorum.

FIG. 1. Portion of the spirem with partial longitudinal division, and a few chromosomes.

FIGS. 2, 3, 4, 5. Early stage in the formation of the chromosomes just after the segmentation of the spirem, showing, in some, openings along the middle line, in others the ends forked, indicating the line of longitudinal division. Pairs of deeply staining chromatin masses are evident in some of the chromosomes, frequently four pairs, or eight masses in a single chromosome.

FIGS. 6, 7, 8, 9, 10. The nuclear membrane has disappeared, and the chromosomes are being drawn up to the nuclear plate.

FIGS. 11–17. Various figures showing the metaphase stage, the orientation of the chromosomes in the nuclear plate; in some, as in *fig. 11* and *17*, the four paired masses of denser chromatin are well seen; in *fig. 17* the pull of the spindle threads is drawing out the middle portion on either side of the broad chromosome, the first step in the separation of the longitudinally divided segment.

FIGS. 18, 19. Two different stages in the separation of the chromosomes in the V form as they are pulled toward the poles.

FIG. 20. Cell plate formed after first mitosis, and U or horseshoe-shaped chromosomes lying in position as they approached the poles.

FIGS. 21, 22. Oblique view of two poles, to show the position of the chromosomes as they come to the poles; in *fig. 21* the group has already elongated somewhat in the direction of the axis of the spindle for the second mitosis.

FIGS. 23, 24, 25, 26. Position of the chromosomes in the daughter nucleus after first mitosis; nuclear membrane formed.

FIG. 27. Nuclear membrane has disappeared at the prophase of the second mitosis, and the chromosomes, still showing the form and characters present when reaching the poles after the first mitosis, are beginning to move to the nuclear plate of the second mitosis.

FIGS. 28, 29, 30. Later stages as the chromosomes are approaching the nuclear plate. The U form is closing up by the folding of the arms, and in some, transverse division has taken place so that they form a pair of rods; in a few the ends of the arms have met and form a ring, which simulates the form of chromosomes in the heterotypic division.

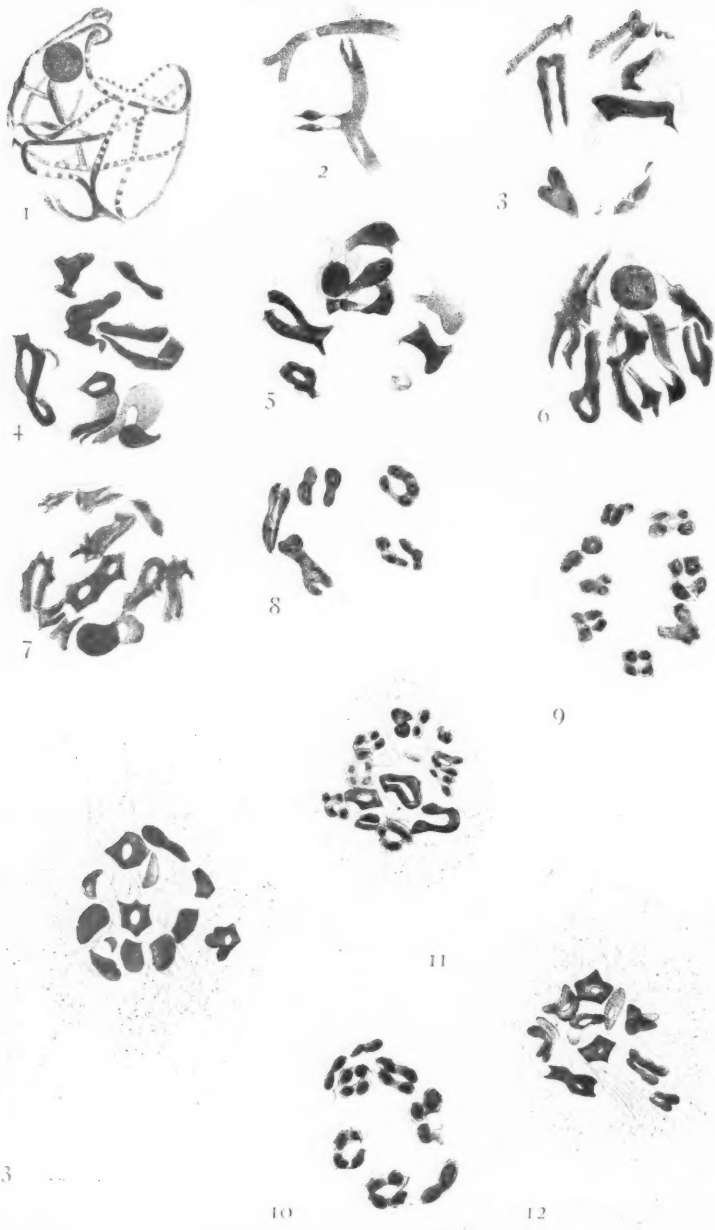
FIG. 31. End view of nuclear plate stage in second mitosis.

FIG. 32. Side view with spindle established, the chromosomes presenting much the same form as in the first mitosis, from the closing up of the arms of the U and the cross division at the junction of the arms.

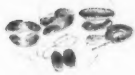
FIGS. 33, 34, 35. Different stages in the separation of the transversely divided chromosomes at the nuclear plate in second mitosis.

FIG. 36. Three different forms of the chromosomes as they are passing to the poles in the second mitosis; the V form; hooked, or J form; and the rod form, depending on the point of attachment of the spindle threads; all in the same nucleus.

FIGS. 38, 39. End view of spindle showing chromosomes approaching the poles at the close of the second mitosis.



ATKINSON on REDUCTION of CHROMOSOMES



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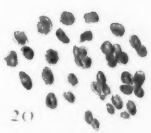

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ATKINSON on REDUCTION of CHROMOSOMES

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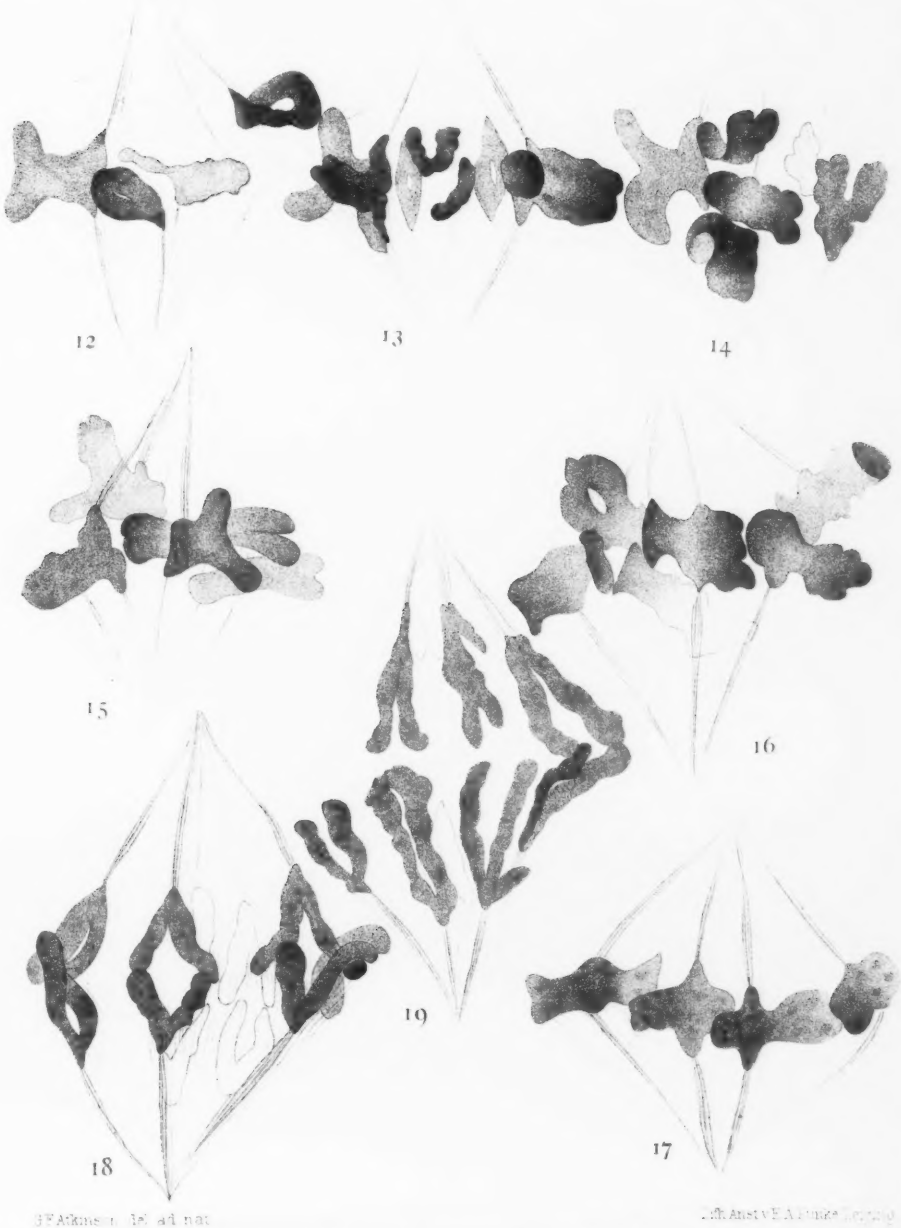

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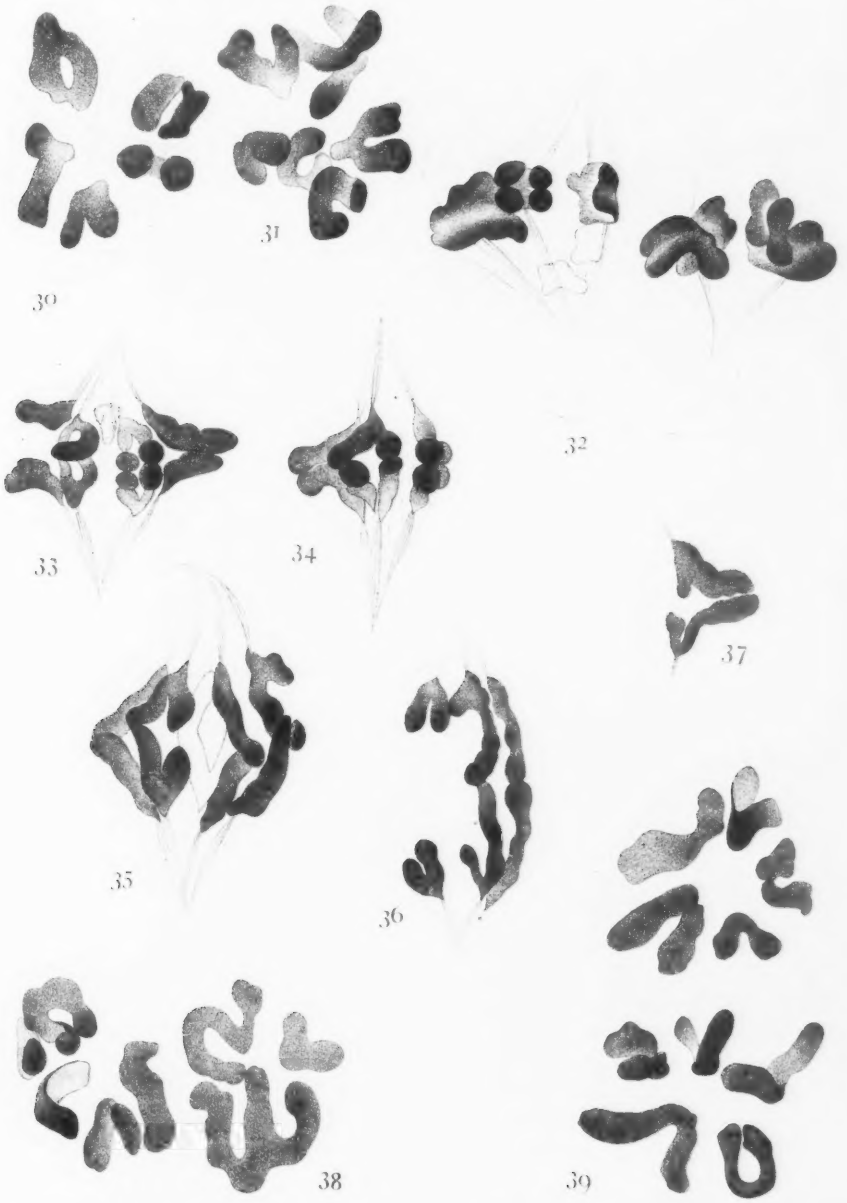

ATKINSON on REDUCTION of CHROMOSOMES

FLOWERS AND INSECTS. XIX.

CHARLES ROBERTSON.

I. *Comparison of the genera of bees observed in Low Germany and in Illinois, with the number of species of each and their flower visits.*—The results credited to Müller are taken from the *Fertilization of Flowers*. They are based on observations made by Herr Borgstette at Teklenburg, in the north of Westphalia, and by Müller at Lippstadt and in Sauerland, in the central and southern parts of the same region, as well as observations made by him in Thüringia. My results are based on observations made within ten miles of Carlinville. Each species of bee is credited with a visit for each of the species of plants on whose flowers it has been taken.

II. *On the flower visits of oligotropic bees.*—Those bees which visit a wide circle of flowers Loew[1] calls polytropic. On the other hand, the bees which restrict their visits to a few flowers he calls oligotropic. Cases are given by quite a number of authors, but, as far as I can learn, they are cited as mere curiosities; and, as if to keep them more interesting by surrounding them with mystery, the facts which give them significance are omitted. The fact that a species of bee is found on the flowers of one or a few species of plants may only indicate that the bee is rare, or that the entomologist does not know where to look for it. In the economy of the host-bees (those not inquiline) the most important flowers are those from which the female gets the pollen upon which her brood is fed, and we need not trouble ourselves with any cases, or give special names to them, unless it is particularly specified that the female collects the pollen. The more often the female visits a flower without collecting any pollen, the stronger becomes the presumption that there is

[1] Blumenbesuch von Insekten an Freilandpflanzen. Jahr. Bot. Gartens Berlin 3:—. 1884.

	Westphalia and Thüringia		Macoupin County, Illinois	
	No. species	Visits	No. species	Visits
Sphecodes	17	28	12	74
Prosopis	15	88	7	118
Colletes	4	16	14	96
Halictus	32	440	30	961
Augochlora	—	—	5	232
Agapostemon	—	—	4	132
Andrena	51	219	42	419
Parandrena	—	—	1	13
Nomia	—	—	1	7
Panurginus	—	—	9	52
Perdita	—	—	1	3
Calliopsis	—	—	3	39
Rhophites	2	8	—	—
Rhophitoides	1	2	—	—
Halictoides	1	2	1	4
Panurgus	2	16	—	—
Dasypoda	1	7	—	—
Cilissa	3	16	—	—
Macropis	1	4	1	6
Ceratina	1	3	2	154
Xylocopa	—	—	1	2
Eucera	1	15	—	—
Emphor	—	—	1	4
Melissodes	—	—	18	266
Synhalonia	—	—	4	83
Xenoglossa	—	—	2	5
Entechnia	—	—	1	5
Anthophora	5	32	5	52
Saropoda	1	9	—	—
Melecta	2	3	1	1
Bombomelecta	—	—	1	1
Crocisa	1	1	—	—
Epeolus	1	2	12	113
Nomada	21	85	17	130
Heriades	1	13	3	34
Chelostoma	3	25	—	—
Andronicus	—	1	1	8
Alcidamea	—	—	2	32
Osmia	13	100	10	102
Megachile	9	77	15	225
Chalcodoma	1	1	—	—
Diphysis	1	15	—	—
Anthidium	3	16	1	3
Stelis	3	12	2	7
Coelioxys	6	28	7	66
Neopasites	—	—	2	4
Bombus	13	457	8	456
Psithyrus	4	52	3	12
Apis	1	189	1	157
Totals	205	1,981	251	4,078
Not accounted for		210		
		2,191		

another flower which she does visit for that purpose, and which, therefore, holds a more important relation to her species. Accordingly, I propose to consider those examples in which the female collects pollen of one species, or several species of the same genus or natural family, the relationship of the plants being such as to give significance to the cases. On the other hand, if a bee uses the pollen of only two plants of different families, I assume that it is essentially polytropic, and that the few visits are merely connected with the fact that it is rare or has a short flight. Of course there still remains a strong contrast between the visits of a bee which flies only a month or two and one which flies throughout the season. As a rule, if a bee has a long flight it must be regarded as polytropic, unless the flowers on which it depends have a long blooming time. Of the thirty-nine species of Halictus and the allied Augochlora and Agapostemon, I regard only one as oligotropic, *Halictus nelumbonis*. It has a comparatively short flight, while the blooming seasons of the Nymphæaceæ are long. When a genus of plants has more than one closely allied species, the difference between a monotropic and an oligotropic bee may depend merely upon the accident that only one species occurs in the neighborhood. My observations show that an oligotropic American bee will gather the pollen of a closely related introduced European plant of the same genus.

The relations of the host-bees to the flowers from which they get pollen are quite analogous to the relations of parasites to their hosts, of phytophagous insects to their food plants, or of predaceous insects to the insects upon which they feed or with which they provision their nests. How the bees maintain these relations is much easier to understand, since the flowers are modified in such a way as to facilitate their visits.

Any ecological position is of advantage only to a limited number of individuals. As soon as this *optimum* number is passed, anything which will enable a set of individuals to get along without coming into competition with the dominant form will be of advantage to them, and their preservation will depend upon their adopting this course. A characteristic which would

be a disadvantage before the *optimum* is reached, may be an advantage after the *optimum* is passed. Whatever may be the characteristic which enables this set of individuals to hold its own in a new ecological position, I think the principal circumstance which accounts for the adoption of a new mode of life is the pressure of competition. The dominant form retains the original position, the other becomes modified (specialized) in adaptation to the newly acquired position.

In my neighborhood there are thirty-five species of Andrena, which complete their flight from March 17 to July 14. These succeed one another, so that not more than twenty-one would be in competition at the same time, if their habits were the same. Ten begin their flight in March, seventeen in April, seven in May, and one in June.

Of thirty-three species whose habits are pretty well known, nineteen are polytropic and fourteen oligotropic, in the sense in which I use those terms. Four of the oligotropic species get pollen from plants of the same genus, but each of the other ten has its own flower, so there are eleven sets which are absolutely without competition among themselves. I think it is clear that so many species could hardly flourish in the same locality and complete their flight in so short a time, if all were in competition for the pollen of the same flowers.

The average maximum flight of the females is forty-eight days. Now suppose that, on account of the pressure of competition, one of these shifts to a different phenological position. Of the flowers whose pollen is so situated that the bee can readily collect it, only those are available whose pollen is produced in abundance between the time the female is impregnated and the end of the time of flight. To use human terms, the bee must choose between a limited number of flowers, and is in no wise free to regulate its habits according to mere whim.

From the above considerations I do not accept the views of Kerner,[2] although they are the ones adopted by Knuth[3] to

[2] Natural History of Plants **2**: 206. 1894.

[3] Handbuch der Blütenbiologie **1**: 106, 114. 1898.

explain such cases. Kerner says: "The flowers of the common bryony, *Bryonia dioica*, are not less remarkable. They occur on two kinds of plants, *i. e.*, on one plant are developed only staminate and on the other only pistillate flowers, and since the pollen is not powdery, and therefore not scattered by wind, it must be carried by insects from plant to plant if the ovules are to mature. But the flowers, especially the pistillate ones, are very insignificant, green in color, with faint smell, and they are half hidden under the foliage. Many insects fly past them without noticing them. They are almost exclusively visited by one of the Hymenoptera, viz., *Andrena florea*, and it can find them in the most out-of-the-way places. This can hardly be accounted for except by supposing that the scent of bryony flowers is perceived by these particular bees and not by other insects." He admits these conclusions must be accepted with discretion. *Andrena florea* gets its pollen exclusively from staminate plants of bryony. How much better do we understand the case if we admit that the scent of the flowers is perceived by the bee? The mud-dauber makes its nests of mud and fills them with flower-spiders, which are so near like the color of the flowers which they frequent that they are enabled to capture their prey by lying in wait. Do we explain the case if we say that Pelopœus perceives the scent of mud and Thomisidæ?

As for out-of-the-way places, my observations indicate that, as a rule, oligotropic bees nest in the neighborhood where their food plants occur, and that, when the brood emerges next year, it finds the flowers in bloom, and that near by.

As a typical case of an oligotropic bee, *Emphor bombiformis* may be mentioned. Both sexes occur in abundance on flowers of *Hibiscus lasiocarpus*, the female collecting the pollen, the males often spending the night in the flowers. The bees do not occur except when the Hibiscus is in bloom. Within several yards of the Hibiscus I have seen the female making nests in a dry bank, carrying water to soften the earth she was excavating. The bees coming out next year find the Hibiscus in bloom near by. The only visits to other flowers I have seen the bees make were to

those in the neighborhood of the Hibiscus. Thus I have seen a single female sucking the nectar of *Cephalanthus occidentalis*, and another that of *Vernonia fasciculata*, as well as a single male sucking nectar of *Ipomœa pandurata*. The outside visits in no way modify the essential relation of the bee to the Hibiscus. For myself, I do not believe in the absolutely exclusive visits of oligotropic bees to their pollen flowers, and I see no reason why they should be expected. If the plants from which a bee gets pollen are common and widely distributed, the proportion of flowers to which it occasionally resorts is much greater than in a case like Hibiscus. Indeed, it strikes me that it is an advantage for the males and unimpregnated females to visit other flowers and not interfere with the females which are collecting pollen. Some bees which stick their pollen with honey get the pollen from nectarless flowers, and so are compelled to visit other flowers for nectar. I have seen *Macropis steironematis*, with pollen balls on her legs, sucking nectar of *Melilotus alba*.

In case of this Macropis and Steironema, Kerner might say the bee perceived or liked yellow flowers, but all of the accessory visits I have seen this bee make were to white flowers, Ceanothus, *Melilotus alba*, Apocynum. In these cases Steironema was in bloom in the neighborhood.

I shall now give the cases of oligotropic bees mentioned by Lubbock,[4] on authority of Müller; by Loew,[5] on authority of Schmiedeknecht; and by Knuth[6] from various sources.

Andrena florea	visits	exclusively	Bryonia dioica.
hattorfiana	"	"	Scabiosa (Knautia) arvensis.
Halictoides	"	"	Campanula spp.
Cilissa melanura	"	"	Lythrum Salicaria.
Macropis labiata	"	"	Lysimachia vulgaris.
Osmia adunca	"	"	Echium.

[4] British Wild Flowers in Relation to Insects 21. 1875.

[5] Blumenbesuch von Insekten an Freilandpflanzen. Jahrb. Bot. Gartens Berlin 3:274 (72). 1884.

[6] Handbuch der Blütenbiologie 1:114. 1898.

Andrena nasuta	visits	Anchusa officinalis.
cineraria	"	Salix.
lapponica	"	Vaccinium.
cettii	"	Scabiosa (Knautia).
hattorfiana	"	Scabiosa.
florea	"	Bryonia.
alpina	"	Campanula.
curvungula	"	Campanula.
austriaca	"	Umbelliferæ.
lucens	"	Umbelliferæ.

Andrena florea	visits	exclusively	Bryonia dioica.
hattorfiana	"	"	Scabiosa (Knautia) arvensis.
cettii	"	"	Scabiosa (Knautia) arvensis.
nasuta	"	"	Anchusa officinalis.
Bombus gerstaeckeri	"	"	Aconitum lycoctonum.
Cilissa melanura	almost	"	Lythrum Salicaria.
Macropis labiata	"	"	Lysimachia vulgaris.
Osmia adunca	"	"	Echium.
cementaria	"	"	Echium.

Andrena florea, mentioned in the three lists, collects pollen of bryony and has been found on no other flowers.

Andrena hattorfiana: both sexes visit *Scabiosa arvensis*, the female collecting pollen. Müller found a female on *Dianthus carthusianorum* and a male on *Jasione montana*.

Halictoides dentiventris: Müller captured both sexes on *Campanula rotundifolia* and *trachelium*, but not collecting pollen. He says that at St. Petersburg Morawitz found it only on Campanula. In the Alps, Müller observed this species collecting pollen of *Potentilla grandiflora* and *Hypochæris uniflora* and visiting seven other flowers.

Cilissa melanura collects pollen of *Lythrum Salicaria*, the males sucking. Müller saw the female sucking on flowers of *Leontodon hirtus*.

Macropis labiata: males and females visit *Lysimachia vulgaris*, the females collecting pollen. Males suck on *Œnanthe fistulosa*, *Rhamnus frangula*, *Rubus fruticosus*.

Osmia adunca: Müller saw both sexes on *Echium vulgare* and says it feeds its young exclusively on honey and pollen of

Echium, but under *Vicia Cracca* this species is indicated as collecting pollen. In the Berlin garden Loew found it collecting pollen of *Nepeta Mussini*. In the two latter cases there is some error, or the bee is not oligotropic. So of the cases mentioned by Lubbock, only one is exclusive, and two are not even oligotropic.

Andrena cettii: females collect pollen of *Scabiosa arvensis*.

Bombus gerstaeckeri: why Knuth says this species visits exclusively *Aconitum lycoctonum* I do not know, for on page 191 it is distinctly stated that the males and workers visit *A. Napellus*, but nothing is said about pollen-collecting.

Osmia cementaria: males and females suck and collect pollen on *Echium vulgare;* males suck on *Trifolium arvense*.

Of the cases mentioned by Knuth, excepting *Andrena nasuta*, only two are exclusive. *Osmia adunca* and *Bombus gerstaeckeri* are not good cases. In the other cases the females collect the pollen exclusively from the plants set opposite them, and the cases are not essentially modified by occasional visits for nectar to other flowers. I hold that *Macropis labiata* is as good a case as *Andrena florea*.

Of the cases mentioned by Loew, three have been passed upon. I know of nothing against any of them except *Andrena cineraria*. The female collects pollen of Salix, but also of *Taraxacum officinale*, so I should exclude it.

In the observation of the insect visits of flowers correct determinations are very important, for otherwise the records are wrong. One has to be sure that the bee is actually collecting pollen, for often a female bee will suck nectar from a flower when her scopæ are full of pollen from another species. On the other hand, there is danger of assuming that a bee is oligotropic from too few observations.

A neighborhood where the flora and insect fauna are in their normal condition is more favorable for correct observations on oligotropic bees; for, when the flowers upon which a bee depends become extinct or rare, the bee may disappear or be forced to resort to flowers which originally it did not visit. In most cases the former is more likely to happen.

A bee may be regarded as oligotropic: (1) When the female collects the pollen of the plants in question and is not known to collect pollen of any other plants. (2) When the bee does not occur except during the blooming season of the flowers. If the female is shown to occur after the flowers have quit blooming, the case is very doubtful. (3) When the bee is frequent upon the flowers, and more or less rare upon other flowers, at any rate except in the neighborhood of the food flowers. The case is also doubtful if it is shown that the distribution of the bee extends greatly beyond the plants upon which it is supposed to depend.

In the more satisfactory cases, if any one should say that he had observed the bee collecting pollen from a quite unrelated flower, I would not accept the determination, or, if that were beyond question, the opinion that the pollen came from the flower on which the bee was taken.

Below I give a list of bees which I regard as oligotropic in the above sense. When I have observed the female collecting pollen from more than one species of a genus, I give the genus; when from more than one genus, I give the family. The details will be given elsewhere.

In Prosopis the females are destitute of pollinigerous apparatus, their nests being provisioned with a paste of honey and pollen. I know of no way to distinguish the flowers which the females visit for this purpose from those which they visit in only an incidental way, so I assume that a species of this genus is oligotropic only so long as it is found exclusively on flowers of one species or group. This may be assumed for either sex so long as the condition holds, as in case of *P. illinoensis*, of which I do not know the females. *P. nelumbonis* has always seemed to me to be the best case of an oligotropic Prosopis.

I have never believed that our species of Epeolus were cuckoos of Colletes, because there are more common species of the former than of the latter genus, and their phenological positions do not show the same correlations which exist between Andrena and Nomada, Megachile and Coelioxys. Besides, the maximum of Epeolus does not approximate that of any other

Bee	Plants visited by females for pollen	Number of species	Flowers of same genus visited for nectar	Flowers of same family visited for nectar	Other flowers visited for nectar	Total flowers visited for nectar
Colletes aestivalis	Heuchera hispida	1	—	—	4	4
latitarsis	Physalis	3	—	—	6	6
willistonii	Physalis lanceolata	1	—	—	3	3
americanus	Compositæ	8	—	2	3	5
armatus	"	4	—	1	1	2
compactus	"	8	—	2	—	2
eulophi	"	3	—	3	11	14
Andrena arabis	Arabis lævigata	1	—	—	—	—
erigeniæ	Claytonia Virginica	1	—	—	2	2
geranii	Hydrophyllum appendic'um	1	—	—	2	2
g. maculati	Geranium maculatum	1	—	—	1	1
polemonii	Polemonium reprans	1	—	—	2	2
spiræana	Spiræa Aruncus	1	—	—	3	3
violæ	Viola cucullata	1	2	—	3	5
erythrogastra	Salix	4	1	—	7	8
illinoensis	"	4	1	—	8	9
mariæ	"	4	—	—	6	6
salicis	"	4	—	—	2	2
nasonii	Umbelliferæ	3	—	—	1	1
ziziae	"	5	—	—	—	—
rudbeckiæ	Rudbeckia hirta	1	—	1	—	1
aliciæ	Compositæ	5	—	2	—	2
asteris	"	3	—	—	1	1
helianthi	"	3	—	2	—	2
nubecula	"	4	—	1	—	1
pulchella	"	6	—	2	—	2
solidaginis	"	6	—	1	1	2
Parandrena andrenoides	Salix	3	1	—	9	10
Macropis steironematis	Steironema	3	—	—	3	3
Halictus nelumbonis	Nymphæaceæ	3	—	—	—	—
Megachile exilis	Campanula Americana	1	—	—	6	6
pugnata	Compositæ	4	—	1	3	4
Panurginus labrosus	Rudbeckia triloba	1	—	2	—	2
albitarsis	Compositæ	2	—	4	—	4
asteris	"	4	—	—	—	—
compositarum	"	5	—	3	1	4
labrosiformis	"	7	—	3	—	3
rudbeckiæ	"	4	—	—	—	—
rugosus	"	4	—	2	—	2
solidaginis	"	2	—	4	—	4
Xenoglossa pruinosa	Cucurbita Pepo (cult.)	1	—	3	—	3
Emphor bombiformis	Hibiscus lasiocarpus	1	—	—	3	3
Anthophora walshii	Cassia Chamæcrista	1	—	1	4	5
Perdita octomaculata	Compositæ	3	—	—	—	—
Halictoides marginatus	Helianthus	3	—	1	—	1

Bee	Plants visited by females for pollen	Number of species	Flowers of same genus visited for nectar	Flowers of same family visited for nectar	Other flowers visited for nectar	Total flowers visited for nectar
Mellisodes desponsa	Cnicus	2	1	—	1	2
illinoensis	Lepachys pinnata	1	—	—	1	1
agilis	Compositæ	6	—	12	10	22
americana	"	9	—	2	1	3
coloradensis	"	7	—	6	1	7
pennsylvanica	"	6	—	9	3	12
simillima	"	6	—	12	3	15

genus of bees on which it might be supposed to be inquiline. Then they are more abundant than would be expected of inquiline bees. Mr. Ashmead's observations confirmed my views, and I have never doubted their correctness since I first read an account of them. In *Psyche*, for March 1894, p. 41, he states that he found *E. donatus* making nests in the ground and provisioning them with a honey-paste. Epeolus thus comes under the same category as Prosopis and is treated the same way in the table.

The cuckoo bees of the genus Nomada hold no particular relations to flowers except through their hosts. However, they show considerable differences. *N. vincta*, which is common on Helianthus and was taken once on Coreopsis, is, I think, an inquiline of *Andrena helianthi*, both bees occurring at the same time, in the same neighborhood, and on the same flowers.

Bee	At least females visit exclusively	No. spp.	Other fls. visited by male
Prosopis nelumbonis	Nymphæaceæ	2	—
thaspii	Thaspium aureum trifoliatum	1	—
illinoensis	Umbelliferæ	5	—
Epeolus helianthi	Helianthus grosse-serratus	1	1
compactus	Compositæ	4	—
cressonii	Compositæ	13	3
pectoralis	Compositæ	2	—
pusillus	Compositæ	4	—
Nomada vincta	Compositæ	3	—

III. *Competition of flowers for the visits of bees.*— It is a question to what extent groups of plants adapted to certain kinds of bees should be regarded as in competition and to what extent they should be regarded as mutually helpful. We will suppose a case in which a plant whose flowers may be visited by bees is introduced into a region where all visitors must be acquired. If the region contains no flowers, there will be no bees to acquire. On the other hand, it seems to me that the more nearly the flora retains its original characteristics the more bees there will be and the more chances there will be of the new flower acquiring bees as visitors. My view is that a patch of plants adapted to bees of certain kinds will be more abundantly visited, if it is surrounded by plants depending on bees of the same kinds, than if the neighboring grounds are unoccupied. There will be more of these bees in the neighborhood. In the table there are fifty-two species which get pollen from particular plants. As far as the data are correct, we take it for granted that the presence and abundance of these bees in a given locality depend on the presence and abundance of the flowers from which they get their pollen. One object in making the table is to show that the plants growing in the neighborhood of plants visited by oligotropic bees gain a certain number of bee visits. The table shows that these plants gain 204 visits in this way. It is expected, however, that some of the visits enumerated in the second and third columns will have to be transferred to the first. Excluding these columns, the neighboring unrelated plants gain 116 visits from the proximity of the food-plants of oligotropic bees. It is not likely that a plant suited to the visits of different kinds of bees will show the normal circle of visitors unless it holds its normal position in the original flora.

IV. *On the influence of bees in the modification of flowers.*— The facts indicate that the first entomophilous flowers were visited for nectar. Anemophilous flowers offer such a poor foothold for insects that they are very seldom visited by them, and the pollen, although no doubt palatable to many insects, is so light

and dry that it is apt to be blown away as soon as it is liberated from the anthers. The first step in the development of entomophilous flowers was the secretion of nectar somewhere about the stamens and pistils, correlated with the modification of the flower so as to afford convenient resting places for insects, and the pollen becoming more adhesive, so that it would remain on the anthers after dehiscense and become attached finally to the bodies of the guests. The object of insect visits being the nectar, modifications favoring cross-pollination resulted in the various forms of diclinism and dichogamy. The perfection of nectar-bearing flowers naturally reached a high grade in the less specialized groups of plants, as, for example, the orchids, and was most frequently associated with the less specialized anthophilous insects.

Along with the development of convenient landing places and sticky pollen, there has no doubt been an increasing number of insects which resorted to flowers for pollen. Finally, the most highly specialized of anthophilous insects, the Hymenoptera, gave rise to a still more highly specialized group of insects which adopted the habit of provisioning their nests with nectar and pollen. Along with the acquisition of this habit the bees developed a coat of feathery hairs to which the pollen might cling, these hairs on certain parts of their bodies, as the hind legs and ventral surface of the abdomen, being greatly modified to form special pollen-carrying apparatus called scopæ. Thus the pollen became absolutely essential in the economy of the most highly specialized anthophilous insects. To the flowers, on the other hand, the bees became the most important visitors, because they had to resort to flowers more frequently than other insects, and because they were provided with a coat specially fitted to retain the pollen, and at the same time exerted themselves to get the coat as full of pollen as possible.

That the development of entomophilous flowers with sticky pollen preceded the development of the bees is indicated by the fact that the less specialized bees only collect adhesive pollen. The most highly specialized bees, however, have acquired the

habit of sticking the pollen with honey, and so can use that of anemophilous plants.

Those flowers, however, which, through their nectar and correlated modifications, were the best fitted to use the services of ordinary insects for cross-pollination, were the least fitted to utilize the insects which were the highest product of anthophilous development. Strange as it may seem, the characters which hindered them from availing themselves of these services were the very characters which are considered the highest adaptations for cross-pollination, viz., diclinism, dichogamy, and large size. On the other hand, the forms which have enabled flowers most readily to avail themselves of the services of bees are the very characters which have been interpreted as adaptations for self-pollination and geitonogamy, viz., small size, homogamy, and the aggregation of dichogamous and other flowers in close clusters.

If an insect in search of nectar visits a dicœcious or other diclinous plant, it is not hard to understand how it is likely to visit both staminate and pistillate flowers and readily effect cross-pollination. It is not so certain that a female bee in search of pollen will visit the pistillate flowers in anything like the same degree. Indeed my observations lead me to believe that they do not. I have seen hive-bees in great numbers collecting the pollen of *Salix humilis* and paying no attention to the pistillate flowers. They fairly monopolized the staminate flowers, while the pistillate flowers were visited by an entirely different set of insects. In the table there are six species of bees which get their pollen exclusively from dicœcious species, Salix and *Spiræa Aruncus*. Of the plants furnishing pollen to oligotropic bees, these are the least able to utilize these bees on account of their dicœcism.

Dichogamous flowers are at somewhat of a disadvantage in utilizing pollen-collecting bees from the fact that the bees are more apt to pay attention to the flowers which are discharging pollen and neglect those in the other stage. In *Impatiens fulva* and *I. pallida* I have observed that *Megachile brevis* collects the pollen from flowers in the first stage and avoids those with

receptive stigmas, because she instantly perceives that the anthers are gone. *Apis mellifica* and *Bombus virginicus* do the same when collecting the pollen of *I. fulva*. In *Campanula Americana*, which is also proterandrous, the oligotropic *Megachile exilis* cleans the pollen from the style-brushes before the stigma opens, and avoids the old flowers. In *Lobelia syphilitica* I have seen little bees collecting the pollen which was pushed out of the anther tube before the stigma appeared. In the proterandrous *Monarda Bradburiana* I have seen small bees collecting pollen directly from the anthers, avoiding the old flowers. The strongly dichogamous flowers mentioned in the table are not so well adapted to utilize their special visitors as are the homogamous ones, such as Viola, Psoralea, Hibiscus, Cassia, because in the latter the bees cannot collect the pollen without touching the stigmas.

Some dichogamous flowers may make effective use of the pollen-collecting bees, as in the case of *Nymphæa reniformis*, which, in my opinion, is proterogynous and without nectar. By a sudden bending of the filaments, bees alighting on the anthers are let down into the stigmatic basin before they discover that the pollen is not being discharged. Of course, in other dichogamous flowers the bees may visit the flowers in the pistillate stage before they discover that the pollen is gone, or for nectar, but my observations have convinced me that this is not the rule, for if they do not know exactly what they are doing and how to do it, they act just like it. On their pollen-collecting expeditions they do not make many mistakes or waste much time.

Even some homogamous flowers are so large that the smaller bees may collect their pollen without touching the stigmas. This may not matter so much if the flowers are visited by large bees, which are more effective. But the smaller flower may, in many cases, utilize the large bees as well and the smaller ones better. So I think the influence of the pollen-collecting bees is in favor of the smaller homogamous flowers.

Under the influence of the nectar-sucking, less specialized, anthophilous insects the highest development is found in diclinous, dichogamous, and hercogamous flowers with highly

specialized nectaries and precise localization of pollen contact. In the less specialized plants, this kind of adaptation early reached the highest degree of perfection in the case of the orchids. But, as far as I know, no orchid holds an important relation in the economy of any bee.

Under the influence of the female bees, the most highly specialized of anthophilous insects, the highest development is found in homogamous flowers without nectar, such as Desmodium and Cassia.

Since bees have entered the field, many flowers seem to have been at a disadvantage in gaining their services, because the stamens were so few that they could not offer pollen in paying quantities. And in many cases the stamens were covered by galeæ and carinæ, so that, to collect the pollen, the bee would have to spend much time going to the bottom of every flower. This difficulty was obviated by lengthening the stamens, reducing the size of the flowers, and crowding the flowers so that the bees could run over or around the inflorescences and sweep up immense quantities of pollen. Inflorescences of this kind are found in Cornus, Hydrangea and Viburnum.

Here we find an explanation of the fact that certain Leguminosæ and Labiatæ have abandoned their galeæ and carinæ, exposing their stamens, and contracting their infloresences into head-like or flat-topped clusters, as in Amorpha, Petalostemon, Lophanthus, Mentha, Blephilia, and Pycnanthemum. Contrary to Müller, I think Delpino is right in regarding Mentha as one of the most highly specialized of the Labiatæ, and I incline to the same opinion regarding the above genera of Leguminosæ. These cases are obscured by the fact that the arrangements permit the visits of a lot of less specialized insects. Nevertheless I think the bees have determined the result.

In the case of Lobelia I have mentioned that small bees collect the pollen pushed out of the tube before the stigma appears. In the Compositæ we find plants perhaps best adapted to attract and utilize the pollen-collecting bees, and the table shows that they have among their visitors more oligotropic bees than any

other group of native plants, and that, too, in spite of their dichogamy. If the flowers were greatly scattered, they no doubt would not attract so many bees, and the bees could carry off the pollen and not render any service by visiting the flowers after the stigmas appeared. But, as a result of the reduction of the flowers in size and the crowding of them in heads, we find a circle of flowers, each one of which ejects the contents of five anthers in a convenient mass. Just without is a circle of flowers with protruding stigmas. Bees sweep over the disk, filling their pollen-scopæ with the greatest facility, at the same time effectually pollinating the neighboring stigmas.

As the homogamous flowers have largely been given over as adaptations to autogamy, so the crowded inflorescences have been given over as adaptations to geitonogamy. As a category I do not accept Kerner's *geitonogamy*. Kerner regards most of the crowded inflorescences as adaptations for geitonogamy, and founds a special category for their reception. This is accepted by Knuth and is incorporated in his recent Handbuch.[7] I do not believe in any adaptations for geitonogamy. I do not deny that it occurs, and under pseudo-ecological conditions may be advantageous, but it is only the name of an accident and does not account for any floral adaptations. Kerner does not make a distinction between a structure, or habit, which has a certain effect, and one which may be conceived to be developed for a certain purpose, or selected on a certain condition. He even speaks of a "contrivance for securing hybridization." Under "contrivances whereby the pollen is protected against wet" he says: "In *Podophyllum peltatum* the pollen is sheltered by the bell-shaped flower, but in addition to this the peltate foliage-leaves are also spread out over the flowers and act as umbrellas." Under the category of protection by isolation in water he mentions a number of ordinary water plants and says: "Flies and beetles which come through the air for honey and pollen are welcome visitors, promoting, as they do, a crossing of the pollen; snails, centipedes, etc., are, on the other hand, kept

[7] Handbuch der Blütenbiologie 1 : 51.

back by the water." He gives no evidence that this protection has anything to do with the fact that the plants have acquired an aquatic location. He uses trivial and accidental effects as a basis for interpretation of all kinds of ecological phenomena.

While it is true that adaptations for cross-pollination are more apparent in the less specialized plants depending on the less specialized anthophilous insects, it does not follow that the adaptations of the highest plants in relation to the highest insects, though more obscure, are to be interpreted as arrangements for autogamy and geitonogamy.

V. *On the supposed pollen-carrying apparatus of flies and birds.* —In regard to the plumose aristæ of such genera of Syrphidæ as Volucella and Sericomyia, Loew[8] observes that the structure appears of no use to the flies, but is of importance in the transfer of pollen. And he regards them, as well as the hairy coat on the lower part of the face, as an adaptation for carrying pollen. In the same connection he mentions the hairy eyes of certain species, though he does not go so far as to consider this as an adaptation for the same purpose.

In the *Entomological News* **4**: 323. 1895, under the title *Insects as pollenizers*, Mr. J. B. Smith mentions that some Diptera have compound hairs, similar to those found in the Apidæ. The author does not say exactly what he does mean, but I have always regarded the note as implying the view that these hairs were so modified for carrying pollen.

In the *American Naturalist* **28**: 680–681. 1874, Mr. J. L. Hancock speaks of certain "repositories" on the head of the ruby-throated humming bird, and throughout his paper seems to imply that the feathers, etc., are specially modified for carrying pollen. As Mr. Darwin says, proof of the existence of such adaptations would be fatal to the theory of natural selection. I have always regarded these statements as mere teleological curiosities, but in his *Handbuch* Knuth has adopted Loew's views,

[8] Jahr. Bot. Gartens Berlin **6**: 114. 1886.

which has the effect of giving them some standing among the fundamental principles of flower-and-insect ecology.

The existence of branched hairs in the bees may properly be interpreted as an adaptation for carrying pollen, because the bees use them for that purpose, and the importance of the hairs is evident, in view of the economy of the insects. They cannot in any way be interpreted as existing for the benefit of the flowers. It could be of no advantage to flies and birds to carry pollen, since they make no use of it. However, it might be claimed that these guests derived an indirect benefit from the pollination of their favorite plants. But their relations to flowers are not close enough to make their existence depend upon the pollination and preservation of any particular species.

An examination of the inquiline bees will lead to the conclusion that the several genera are not related to one another but have arisen independently from different groups of host bees. It will also lead to the conclusion that they have all lost their hairy coats, or tend to do so, as in Psithyrus. To my mind the fact that these bees began to lose their coats as they abandoned their pollen-collecting habits, involves a clear refutation of the claims that any structures on flies and birds were developed for the purpose of carrying pollen.

CARLINVILLE, ILL.

THE ORIGIN OF THE LEAFY SPOROPHYTE.

JOHN M. COULTER.

ATTENTION has been called afresh to this exceedingly interesting and obscure problem by the discussion of alternation of generations by Professor Bower in his recent presidential address,[1] and in papers of Dr. Klebs,[2] and Dr. Lang.[3] The remarks of Professor Bower are largely in defense of his theory of the antithetic origin of the sporophyte, which had been attacked by Dr. Scott in his presidential address of two years before in restating Pringsheim's theory of homologous alternation. In defending his position, Professor Bower discusses arguments derived from the behavior of algæ and certain fungi, from bryophytes, and from apogamy and apospory. He claims that those algæ and phycomycetes which show subdivision of the zygote into spores appear to offer the "key to the enigma" of the origin of the sporophyte, but he makes no further claim for these "fruit bodies" than that they suggest the way in which the sporophyte may have arisen, his view not at all involving the idea that these "fruit bodies" and the sporophyte are homogenetic. He calls attention to the fact that knowledge of cytological phenomena among algæ and fungi is far too meager, especially in connection with the divisions of the zygote referred to. If reduction is found to occur in connection with the zygote divisions, in such forms as Œdogonium and Coleochæte, there would be a reasonable foundation for the belief that the "fruit bodies" are the correlatives of a sporophyte, the beginning of a neutral generation.

In reference to the bryophytes, Professor Bower sees in them a good illustration of the origin of the sporophyte by "a

[1] Nature, Nov. 17, Nov. 24, Dec. 1. 1898.

[2] Annals of Botany **12**: 570–583. 1898.

[3] Annals of Botany **12**: 583–592. 1898.

progressive antithetic alternation." He calls attention to the remarkable constancy of alternation in this group, apogamy and apospory being singularly absent. This undeviating alternation he suggests may be accounted for by the dependence of the sporophyte, which is in an "equable physiological condition." As a contrast to this, the independence of the pteridophyte sporophyte, and its exposure to varied conditions, may have caused more freely unusual developments. The primitive pteridophyte, however, was probably in a dependent condition, as the embryos of modern pteridophytes are.

Apogamy and apospory Professor Bower would regard as "abnormalities," calling attention to the fact that these phenomena have their "headquarters" in the leptosporangiate ferns, a peculiarly specialized phylum with many other abnormalities. Even when apogamy occurs the archegonia are first produced, indicating the "first intention" of the plant; and in both apogamy and apospory the growths may be very anomalous.

In this connection, Professor Bower makes a very interesting suggestion, based upon the experiments of Dr. Lang and others. He observes that apogamy is induced by prevention of contact with fluid water ("rendering fertilization impossible"), exposure to direct sunlight, and possibly to certain temperature conditions. All this leads to a "plethoric" state, which he thinks may be a necessary condition preceding apogamy, as opposed to deficient nutrition, which precedes apospory, the latter being "a physiological refuge for the destitute plant." He suggests that nuclear changes may accompany these conditions, plethora doubling the chromosomes, and hence inducing the development of a sporophyte; and deficient nutrition reducing the chromosomes, thus making a gametophyte possible. Of course it remains to be proved that nuclear instability, coming to be well recognized, is connected with disturbed nutrition, and also whether a smaller or larger number of chromosomes necessarily determine a gametophyte or a sporophyte.

On the whole, therefore, Professor Bower still maintains that the sporophyte is the result of the gradual elaboration of the

zygote, "a fresh phase having thus been gradually interpolated," in other words, that its origin is antithetic. It would seem that in his opinion the sporophyte has probably appeared in just one way. This does not mean that all sporophyte plants are homogenetic, but that all have had an origin similar to that of the sporogonium of bryophytes. Professor Bower acknowledges that the present tendency is toward a comprehensive polyphyletic view as regards alternation, stating that "when difficulties arise refuge is taken in the plausible suggestion of distinct lines of descent."

Dr. Lang's paper is rather a presentation of current views than an expression of opinion in reference to any of them. He recognizes the fact that the regularity of the zygote product in such forms as Œdogonium and Coleochæte represents a life history decidedly different from the homologous alternation of sexual and asexual plants in most thallophytes. From one point of view this zygote product is merely a reduced asexual individual; from another point of view it is not a reduced asexual individual, but a special adaptation to multiply the product of fertilization. The former is the theory of homologous origin, the latter the theory of antithetic origin. Certainly the facts of morphology do not decide which theory is correct. Dr. Lang calls attention to the fact that in considering alternation the possible polyphyletic origin of the archegoniates must be kept in mind, as the pteridophytes may represent an entirely distinct line from the bryophytes, as suggested by Goebel. In spite of Professor Bower's disposition of apogamy as an argument, Dr. Lang thinks that experiments with this phenomenon indicate so clearly that the gametophyte may assume characters of the sporophyte under suitable conditions, almost a complete series of transitions between gametophyte and sporophyte having been observed, that such a general property of the fern gametophyte cannot be disregarded in the discussion, even though the phenomenon may be called teratological. He thinks that apogamy suggests the homology of the gametophyte and sporophyte, and may suggest how pteridophytes could have

been derived from algæ forms, and how alternation in ferns might have arisen if it did not come antithetically.

The paper of Dr. Klebs deals with the subject of alternation of generations in thallophytes, and therefore concerns this present discussion but indirectly. His experiments among the lower forms, as is well known, have proved that there is no such rigidity in life histories as was once supposed. As a consequence, he does not consider that there is any such thing even as a regular homologous alternation of sexual and asexual phases. He thinks that experiments may prove that the so-called "fruit bodies" of such forms as Œdogonium and Coleochæte may turn out to be the result of certain conditions, rather than an inevitable part of the life history. He seems to consider that the origin of pteridophytes probably has nothing to do with that of bryophytes, and that there is at present no clue whatsoever as to the origin of the former. Such a peculiar structure in common as the archegonium he suggests may be a purely parallel development, without necessarily indicating any phylogenetic connection.

It will be seen from the above papers that, while the origin of the sporogonium of bryophytes seems to be suggested, the origin of the leafy sporophyte is too obscure to justify any definite claim. According to Bower it is most probable that it is developed from such a sporogonium structure as is displayed by the bryophytes today; according to Lang and Klebs there is a possibility that it may have had an entirely independent origin, and may never have been in the sporogonium condition.

It is recognized that there are peculiar difficulties in the discussion of such a subject. Although the morphology of the existing representatives of the various groups is fairly well known, there are two enormous gaps in our knowledge which make a definite conclusion impossible. One of these gaps is the ancient history of the bryophyte and pteridophyte lines. For instance, it is certain that the pteridophytes were well represented in the palæozoic, probably even in its earliest periods. This represents such a tremendous stretch of time that almost any change, however extensive, may have been possible in any given form. It is

not through lack of time, therefore, that one would suggest that it is unlikely for a leafy sporophyte to have been developed from a sporogonium. From the fact that our earliest evidences of the pteridophytes show them to have been about as highly differentiated as they are now, it is evident that the evolution of the line reaches very far back. It is probably hopeless to expect that this gap in our knowledge will be filled.

The other gap is in reference to cytological details. The whole subject of alternation of generations seems to be so bound up with nuclear changes that a knowledge of these in the thallophytes becomes a very great desideratum. This gap in our knowledge is likely to be filled up rapidly. It may be that we have been too rigid in our use of the number relations of chromosomes as distinguishing gametophytes from sporophytes. Be this as it may, there is enough in the testimony associating the doubling and the reduction of chromosomes with the sporophyte and gametophyte stages to justify such use. It would seem that an investigation into the nuclear changes which occur in the "fruit bodies" of such forms as Œdogonium and Coleochæte would go far toward settling the antithetic origin of such a structure at least as the sporogonium of bryophytes.

It is not my purpose in this paper to traverse ground which has been gone over so recently and so ably, but merely to discuss certain facts and possibilities in connection with the leafy sporophyte that may be suggestive. In discussing the origin of such a structure as the leafy sporophyte where there is no possible direct evidence, and where every view must be hypothetical, it seems necessary to consider all possible alternatives. The chief service which these various alternatives render is to coordinate the facts and to suggest lines of research.

No structure among plants seems to have left so little trace of its origin as the leafy sporophyte of pteridophytes and spermatophytes. The evolution of the leafless sporophyte of bryophytes seems traceable from an oospore which directly organizes a group of sporogenous cells. Sterilization of the peripheral cells would result in a simple spore case like that of

Riccia, while further encroachment upon the sporogenous tissue, with more or less differentiation of the sterile tissue, would account for the series of sporogonia displayed by bryophytes. Whether the origin of this structure is to be regarded as homologous or antithetic is not pertinent to the present discussion, but it seems reasonable to see in it an entirely new structure developed by the oospore, and in no way homogenetic or even homologous with the gametophyte. It has been noted that the argument drawn from apogamy in favor of homologous origin finds little or no application among bryophytes, for the origin of the sporogonium seems to be as fixed as the origin of any plant structure can be.

It has been common to regard the distinct sporophyte as having been established once for all by the bryophytes, and the sporophytes of the higher groups to have been derived from those of the bryophytes. In searching for the origin of the leafy sporophyte, therefore, attention has been focused upon the sporogonia of bryophytes, and the Anthoceros forms have been selected as most nearly representing the ancestral condition.

The doctrine that any plant structure, however important, can have but one phylogeny, is hardly tenable at present. That heterospory has appeared independently in several lines has become evident ; and that it has resulted more than once in seed formation is hardly less evident. The conditions which determined these modifications must have been common enough to have established similar results more than once. Why the sporophyte may not fall in the same category is not clear. Professor Bower's statement that the polyphyletic origin of a structure is an easy escape from difficulties suggests caution, but does not close the door to the fact that nature may have found the same easy way out of difficulties.

In contrasting the sporophytes of bryophytes and pteridophytes, they seem to have nothing in common except that they are usually derived from the oospore and represent an asexual generation. These facts are important, but so are the numerous other facts in which they differ sharply. There are also asexual

generations derived from oospores among thallophytes, but regular alternation of sexual and asexual generations is not definitely established. When alternation becomes definite the sporophyte is a recognizable structure, but that this structure must have been established just once or in just one way is far from necessary.

It may be well to contrast the leafless and leafy sporophytes. In the former case the structure is never independent of the gametophyte, develops no lateral members, has nothing comparable to sporangia, and its whole tendency is to render complex the spore-producing region. In the latter case the sporophyte is dependent upon the gametophyte only in its embryonic stage, develops prominent lateral members, has distinct simple sporangia, and its whole tendency is to render complex the sterile or nutritive tissues. As one traces the evolution of the bryophyte sporogonia they give evidence of increasing complexity and hence rigidity, and little promise of originating such a diverse tendency as that shown by the sporophyte of pteridophytes. The mosses are conceded to be a highly specialized, and hence non-productive line, the legitimate outcome of the whole bryophyte tendency. Why the liverwort lines may not also be regarded as highly specialized and hence non-productive does not seem clear. It is true that the Anthoceros forms show a sporophyte tendency unlike the others, and that if such a sporophyte should become independent and put out leaves, and if the continuously developing spore region should be restricted and broken up into simple sporangia which should associate themselves with the leaves, we might have something like the existing leafy sporophytes. But there is no evidence that these things ever happened. On the contrary, the sporophyte of Anthoceros would seem to be as hopelessly specialized as that of other lines. It is true that all the things referred to above may have happened, and Anthoceros may be the nearest living suggestion of the archetypal pteridophyte, but the case is not so clear that our eyes should be shut to other possibilities.

If the bryophyte sporogonium is responsible for the leafy

sporophyte, then it is evident, as Bower has shown, that the leaves of the latter are the result of progressive sterilization, and are secondary structures of the sporophyte. But if some other origin of the leafy sporophyte is possible, the leaves may not have arisen as secondary structures.

It may be well to trace briefly the origin of gametophyte leaves, as exhibited by the mosses, since the sequence of events seems fairly clear, and may prove suggestive. Among the Riccia forms the thallose body produces sex organs and does chlorophyll work with no special differentiation of regions. From this condition there is evident a tendency to segregate the sex organs into definite regions, so that eventually the region of the body devoted to sex organs becomes quite distinct. The differentiation of a sex organ region is still further emphasized by its separation from the rest of the body by being carried up upon a vertical branch, an extreme case being displayed by Marchantia. As a result, the chief chlorophyll work and the production of sex organs are distinctly set apart by the organization of a gametophore arising from the thallus.

The gametophore, primarily a sex organ branch, proves to be more favorable for the display of chlorophyll tissue than the thallus, and the simple leaves of mosses appear, supplementing the chlorophyll work of the thallus. In sphagnums the thallose body continues associated with the leafy gametophore. In the true mosses, however, the chlorophyll work of the gametophyte is more or less given over to the gametophore leaves, and the thallus region is reduced to the so-called "protonema." In a very true sense, therefore, the gametophyte is always a thallus, special vertical or radial branches being developed in liverworts as gametophores, and in mosses as leafy gametophores. The loose habit of homologizing the leafy "moss plant" with a liverwort thallus on the one hand, and a fern prothallium on the other, is not merely bad morphology, but is apt to be very misleading.

The suggestion to be obtained from this history is that leaves may develop in response to more favorable conditions for their work, and such development may result in the great reduction

of chlorophyll work done by the less favored region, and its consequent simplification. It is evident that with the exchange of an aquatic for a terrestrial habit the thallose body would not be a favorable type for chlorophyll work, and that the development of chlorophyll tissue upon erect structures of various kinds might follow. Among bryophytes the erect structure laid hold of is the gametophore, and not the sporogonium. I grant that this same reasoning would make the sporogonium of the Anthoceros forms a specially well adapted erect structure for the development of leaf tissue and hence leaves. The objection, however, is that the sporogonia of bryophytes are most persistently spore-bearing structures and nothing else, every tendency towards more complex organization having spore production and spore dispersal in view; and that such specialized structures are not apt to be productive of new lines of development.

In considering, therefore, whether it is possible to disregard the bryophytes in our search for the origin of the leafy sporophyte, we are largely influenced by the fact that the bryophyte sporophyte, throughout its whole history, is dominated by a tendency which does not appear in the pteridophyte sporophyte. Before the establishment of alternate generations the plant body may be said to have had three functions, namely, chlorophyll work, and the production of gametes and spores. The appearance of the bryophyte sporogonium was dominated by the separation of spore formation from the other functions, chlorophyll work being retained by the gametophyte, along with gamete production. Attention has been focused so long upon the gametes and spores as the two dominant factors in differentiation that it is hard to conceive of the possibility of the domination of another factor. It is entirely conceivable, however, that another form of differentiation may have occurred, dominated by the needs of the chlorophyll work, and not by spore production. Certainly a great need for change, when aquatic conditions were exchanged for terrestrial, was in connection with the display of chlorophyll tissue. It would seem as if the bryophytes had laid emphasis upon spore production, and therefore never became

organized for the fullest use of terrestrial conditions; while the pteridophytes laid emphasis upon chlorophyll work, and became highly organized for terrestrial life. It would seem possible, therefore, with the three factors to take into account, that two distinct asexual lines may have been organized, distinct in the factor selected to dominate.

Such a conception may be simple enough, but it is hardly worthy of consideration without more practical statement. If more favorable structures can be developed in response to the needs of spores or gametes, there seems to be no good reason why more favorable structures may not be developed in response to the needs of chlorophyll work. If such a response in structure is possible, it would naturally express itself first in developing the largest display of chlorophyll tissue in the most favorable region of the body, which would gradually become differentiated more and more distinctly from the rest of the body. It does not seem clear why the appearance of an erect leafy axis, bearing neither gametes nor spores, is not quite as supposable as the appearance of a sporophore with neither gametes nor leaves, or a gametophore with neither spores nor leaves.

Of course such a leafy axis would be an integral part of the thallus body from which it was developed, and in no sense a distinct "generation," any more than the leafy gametophore and the protonema of mosses are distinct generations. Upon such a leafy axis spores would find a more favorable position than upon the ordinary thallus body, and eventually they would be segregated upon the leafy axis, developing in connection with chlorophyll tissue just as they had in the thallus body. In such conditions comparatively simple sporangia would be developed, being entirely subordinated to the nutritive tissues. A parallel case is found in the gametophore of mosses, which also prove favorable for leaf development; or even in the sporogonia of certain bryophytes, which also prove favorable for chlorophyll tissue, but this is rigidly subordinated to the work of spore production.

With the development of a leafy axis bearing spores, there is

no reason why it should not become independent of the thallus body which produced it, as the leafy gametophore of mosses becomes independent of the protonema. The great difference in the final result in the two cases arises from the fact that in mosses the protonema is without gametes or spores; while in the case we are supposing the thallus body produces gametes, and the leafy axis spores. That a thallus body can directly produce just such a leafy axis bearing spores is testified to by the numerous cases of apogamy observed among pteridophytes. In fact, the theoretical life history we have been tracing is concretely represented by the life history of a fern in which apogamy has occurred.

If the phenomenon of apogamy represents the primitive status of the leafy sporoyhyte, it remains to imagine how this spore-bearing leafy axis could have become the usual product of the oospore. We find no trouble in believing that the usual oospore product frequently appears apogamously, for this has been demonstrated; but to imagine a general primitive apogamous habit of origin gradually passing into a predominant oospore habit of origin is difficult. In the condition supposed, namely, a thallus body producing gametes, and a special leafy axis bearing spores, zygotes and spores would have the same power, the germination of each resulting first in the thallus body and afterwards the leafy axis. If real alternation can be brought about by such a condition, the thallus portion of the zygote product and the leafy axis portion of the spore product must be gradually eliminated. In other words, the tendency would be to eliminate that particular region which is concerned in producing the reproductive body. Perhaps such a tendency is no more difficult to understand than the fact that a spore produces a gametophyte rather than a sporophyte, and a zygote produces a sporophyte rather than a gametophyte. A common explanation has been that a zygote, for some reason, stops reproducing the plant body which organizes it, and begins to produce an entirely new structure, which certainly seems to have been the case in the formation of the sporogonia of bryophytes. It would seem no

more difficult for a zygote to stop producing one distinct portion of the plant body, and to continue producing the other.

Why in both cases it tends to produce the structure less immediately related to it, rather than the one which has originated it, is a question which cannot be answered at present. Cytology may offer certain suggestions, but they are vague as yet. The fact that the chromosomes are doubled in number by the process of fertilization, and are reduced again in the sporogenous tissue may have some bearing on the question. It seems clear that in all life histories where the sexual act occurs there must be a corresponding reduction division somewhere. In distinct alternation of generations, the "doubling" and the "reduction" are associated with the two generations. But before distinct alternation was established "doubling" and "reduction" must have occurred, and there is no present reason to doubt that in such case reduction often, if not generally, occurred in connection with the development of spores. When, therefore, the zygote was restricted to one region of the body, and the spore to a very distinct region, the alternation of "doubling" and "reduction" might well develop into an alternation of generations.

The very interesting results obtained by Strasburger and Farmer in their study of Fucus, which show that the reduction division in that plant occurs in connection with the development of the sex organs, may be correlated with the absence of spores. Such an observation emphasizes the fact that reduction must occur somewhere, and if sporogenous tissue is not developed, it would seem more likely to occur in gametogenous tissue, representing a new cell sequence, than in ordinary nutritive tissue.

With such an origin of the leafy sporophyte, it would follow that foliage leaves are not secondary, but primary structures, and that sporophylls have arisen from the differentiation of foliage leaves bearing sporangia, a state of things certainly suggested by the most primitive pteridophytes known. It would further follow that the evolution of the strobilus has followed the development of foliage leaves, a view in accordance with the older morphology. Such a view would make intelligible the

great "gap" recognized as existing between bryophytes and pteridophytes, as the two groups would not be phylogenetically connected, and would have developed along very divergent lines from the first. It would mean that at least two independent sporophyte lines have appeared, the bryophyte line probably with an antithetic origin, and the pteridophyte line possibly with an homologous origin. The great prominence of the latter line, with its spermatophyte sequence, is correlated with the development of a vascular system, and it would seem as though the evolution of an elaborate vascular system must have depended upon the domination of chlorophyll work.

Perhaps one of the strongest arguments against the polyphyletic origin of archegoniate plants is the constant character of the archegonium. It would seem to some inconceivable that an organ so definite and so characteristic, and so unlike anything in thallophytes, could have appeared in two independent lines. However, the possibility of two independent appearances of such an organ would depend upon its origin, a subject of great obscurity. That it has been derived in some way from the oogonium of thallophytes seems hardly to be questioned, and that it is one of the results of the exchange of aquatic for terrestrial habits seems hardly less doubtful. That the archegonium represents a group of oogonia protected by a layer of sterile tissue seems to be a reasonable suggestion, and that the differentiation of this sterile protective layer into neck and venter would follow naturally from the exclusive functioning of the innermost oogonium seem probable enough. The conditions which induced this protection of aggregated oogonia, however, could hardly be claimed to have resulted but once in an archegonium.

It must be acknowledged that if the leafy sporophyte has had any such origin as has been indicated above there is no algal evidence that can be presented, as in the case of the leafless sporophyte. It must be remembered, however, although it may be regarded as a convenient refuge for all theories of phylogeny, that we are dealing with a structure whose origin is very ancient. Why the algæ continue to give suggestions as to

the origin of the bryophyte sporogonium, and, so far as known, give no intimation of the independent origin of the leafy sporophyte, is a pertinent question. It seems to be also true, however, that the bryophytes give no clear suggestions as to the origin of the leafy sporophyte, and we are left to imagine the method of its origin from either group.

In thinking of this possible disconnection of the bryophyte and pteridophyte lines, it may be well to recall the similar experience of the gymnosperm and angiosperm lines. Certainly the gymnosperms and angiosperms seem to have more characters in common than do the bryophytes and pteridophytes, and seem to be more insistent in their demand for a common phylogeny; yet that the gymnosperms represent at least one independent phylum can hardly be longer doubted.

All such discussion is, of course, very vague and general, and may not commend itself to many as profitable. But it serves its purpose in stating the problem, and in presenting the possible alternative solutions. We have been in danger of restricting the operations of evolution too rigidly, making the lines of advance too few, and forgetting the possibilities of change during the enormous stretches of time. The polyphyletic origin of similar structures and of similar groups makes the problems of phylogeny immensely more complex, but is probably much more consistent with the facts.

THE UNIVERSITY OF CHICAGO.

BRIEFER ARTICLES.

THE SEEDLINGS OF *JATROPHA MULTIFIDA* L. AND *PERSEA GRATISSIMA* GÄRTN.

(WITH SIX FIGURES)

TWO MODES of germinating are characteristic of the dicotyledons, with the cotyledons above or under ground. The first is undoubtedly the commonest. In this case the cotyledons, as a rule, are freed from the seed-coat and develop as two, seldom only one or several, leaf-like organs. In the other case, however, the cotyledons either remain enclosed in the seed or become free, but stay under ground. These are the principal forms of germination which Klebs[1] has ascribed to the dicotyledonous orders, and it is interesting to see that both forms may occur not only within allied genera, but even among species of the same genus. Furthermore, the germination itself exhibits a number of biological variations in regard to the relative development of the primary root, the hypocotyl, and the cotyledons. But it would seem very difficult to find any deviation from the rules given above, at least from the first, in which the cotyledons are above ground and free, while the second comprises two possibilities, enclosed or free cotyledons. When the seed-leaves are carried up above ground, this is not necessarily connected with the development of a hypocotyl, nor are the underground seedlings always destitute of such. But when a long hypocotyl raises the seed above the ground and the cotyledons, furthermore, are provided with petioles of considerable length, we should never expect to find the seed-leaves permanently enclosed in the seed and falling off without being exposed to sunlight. It would seem very strange if any such case really existed.

It was, therefore, very surprising to learn that Fr. Müller, in Blumenau, Brazil, had discovered a plant which exhibited this peculiar mode of germinating, the *bicuiba* or *Myristica Bicuhyba*, a tree of the primeval forests in Brazil.[2] The seedling of this tree possesses a long

[1] KLEBS, GEORG: Beiträge zur Morphologie und Biologie der Keimung. Untersuch. aus d. Botan. Inst. Tübingen 1: 536–635. 1885.

[2] MÜLLER, FR.: Keimung der Bicuiba. Berichte d. deutsch. botan. Ges. 5: 468. 1887.

hypocotyl and two deeply lobed cotyledons, which, although above ground, do not leave the seed. To this instance may, however, be added a second, but of an order very remote from the Myristicaceæ. A few weeks ago Mr. G. W. Oliver, of the botanical garden at Washington, D. C., called my attention to some very odd-looking seedlings of *Jatropha multifida*, which were kindly submitted to the writer for closer study. The germination of this plant had, so far, only been very briefly mentioned by Sir John Lubbock,[3] who merely recorded it as an exception from that of the other Euphorbiaceæ. The seedling develops as follows.

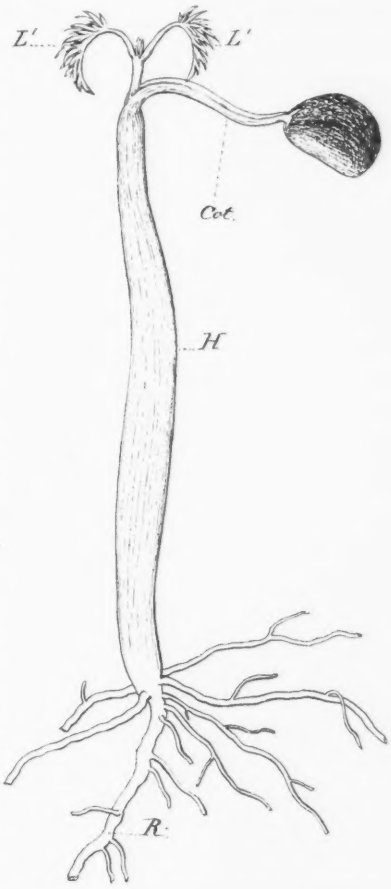

FIG. 1.—Seedling of *Jatropha multifida* L.; natural size.

Next to the primary root the hypocotyl increases very considerably in length and penetrates the soil by making a strong curvature until the seed becomes raised above ground, while simultaneously the petioles of the cotyledons have reached their final development and attained a very considerable length. While the hypocotyl increases rapidly in length and thickness, the cotyledons show no signs of becoming freed from the seed-coat. The plumule begins to develop a distinct internode, and the first leaves, being opposite and of approximately the same shape as the later ones, appear a short time before

[3] LUBBOCK, J.: Seeds and seedlings.

the cotyledons drop off, with their leaves still enclosed. The accompanying drawing (*fig. 1*) illustrates a seedling with the cotyledons, *Cot*, attached, and the first leaves, L^1, almost expanded. The primary root, *R*, is persistent and branches very soon, while a few secondary ones proceed from the base of the hypocotyl. The very long and thick hypocotyl, *H*, is green and glabrous; there is an early development of cork-layers; the bark-parenchyma is broad and traversed by a number of laticiferous ducts. The mestome bundles are of normal structure and between these are numerous strata of interfascicular cambium. A pith occupies the center of the hypocotyl; its cells are like those of the bark, thin-walled and filled with starch, but there are no laticiferous ducts. As stated above, the cotyledons have long petioles and their blades (*fig. 2*) are mostly oblong with a short point, but without any lobation as was observed in *bicuiba*. They are somewhat fleshy and pale in color; nevertheless, stomata are present on the upper surface and not on the lower. Along the ribs on the upper face, two kinds of hairs are visible. These are either long, multicellular, and pointed, or unicellular and almost globular in shape. The latter (*fig. 3*) are quite abundant in contrast to the first, and in some places they covered the surface just above the ribs. They represent glandular hairs, but their function could not be ascertained. The lower surface of the blades, which lie close up to the endosperm, is wholly glabrous. A typical palisade tissue was observed, covering a rather dense pneumatic tissue, and both contained abundant deposits of starch; laticiferous ducts were also very frequent.

FIG. 2.—Blade of a cotyledon; natural size.

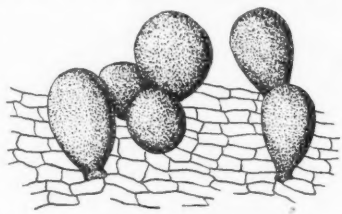

FIG. 3.—Epidermis with glandular hairs from the cotyledons of *Jatropha multifida*. × 240.

This seedling has no mate among the other species of Jatropha, which have been studied heretofore. Sir John Lubbock figures and describes *J. Curcas* L. and *J. podagrica* Hook., both of which possess stout and long hypocotyls; furthermore, their cotyledons are free and provided with distinct petioles, although not equaling in length those of *J. multifida*.

Another and very peculiar manner of germinating was observed in *Persea gratissima* Gärtn., of which several seedlings were cultivated at

the same time in the botanical garden at Washington, D. C. It is strange that the Lauraceæ have been almost entirely passed by in works dealing with seedlings, none having been recorded either by Klebs (*l. c.*) or Sir John Lubbock (*l. c.*). Schacht[4] appears to be the only author who has given us some information about them; he states that the seed of *Persea gratissima* germinates while the fruit is still attached to the tree. This author observed, also, that in this species of Persea the plumule attains a very early development with a number of leaves, similar to Juglans and Tropæolum. Having detected a few other peculiarities connected with the germination of Persea, and having been unable to find any figure of this, I take this opportunity to publish and illustrate my observations, together with the still more remarkable case of germination just described.

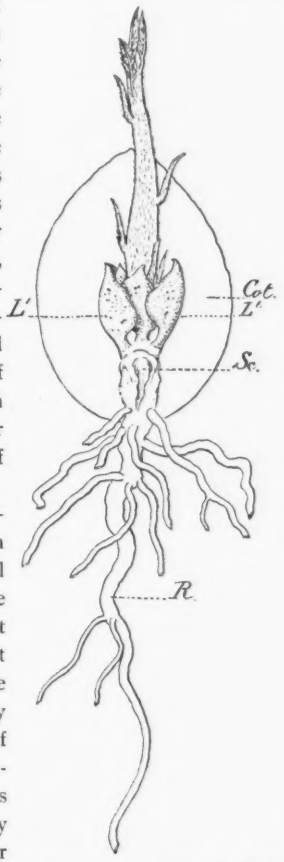

FIG. 4.—Seedling of *Persea gratissima* Gärtn., natural size. *R* primary root; *Sc*, scar from the removed cotyledon; *Cot*, the other cotyledon; L^1, the first leaves.

In *Persea gratissima* there is no endosperm, and the large cotyledons remain enclosed by the seed-coat. No hypocotyl develops during the germination, but the plumule grows out very soon as a shoot with several leaves, while the primary root at the same time has attained a considerable length and developed a number of very strong lateral roots arranged in whorls of from three to five or more. In the accompanying drawing (*fig. 4*) the plumule has developed as a single shoot, and it is very strange to notice that the very first four leaves, L^1, are not only opposite, but even provided with petioles and blades, thus imitating the typical leaf of this species. On the other hand, the succeeding five or

[4] SCHACHT, HERMANN: Lehrbuch der Anatomie und Physiologie der Gewächse 2: 447, 468. 1859.

six leaves are almost scale-like, with no petiole or blade, but covered with silky hairs like the axis and the proper leaves when young. Thus *Persea gratissima* demonstrates the fact that in seedlings with enclosed cotyledons, there may be an alternation of various forms of leaves, while in Juglans and Carya, for instance, all the first leaves are scale or bristle-like.

When, however, the plumule does not develop as a single shoot but as a complex of ramifications, the first leaves become almost suppressed and appear only as small and rather broad scales (*fig. 5*). In this case, the shoots have pushed out very freely from the axils of the lowest leaves, and have almost attained the same development as the plumule itself, possessing elongated internodes and some narrow scalelike leaves with silky hairs. Besides these lateral branches, there is a bud observable in the axil of each of the two cotyledons (*fig. 6*), which is evidently ready to develop if the mother-shoot, the plumule, should become injured. The first developed leaves were perfectly glabrous, in contrast to the succeeding ones. There were a few stomata on the lower surface, but none on the upper. The mesophyll formed a homogeneous tissue filled with starch, and there was no indication either of collenchyma or stereome above or underneath the mestome bundles.

FIG. 5. – Plumule of seedling of *Persea gratissima;* natural size.

FIG. 6.— A bud from the axil of a cotyledon of *Persea gratissima*. L^1, L^2, L^3, the first, second, and third leaf; magnified.

In Lindera and Sassafras, at least in their North American representatives, the germination takes place underground, but the plumule develops as a single shoot. The first leaves are bristle-shaped, succeeded by a few whose shape is approximately the same as that of the typical leaf. The three-lobed leaf of *S. officinale* Nees, however, is only seldom observed in the first year of the seedling, those developing at this stage being ovate and entire.—THEO. HOLM, *Brookland, D. C.*

ON THE BLIGHT OF SORGHUM.

THE tissues of the different organs of sorghum, under certain conditions which are not as yet perfectly known, may become the seat of an intense production of red pigment which impregnates them. The cells die and disintegrate, the disease being known as sorghum blight (*sorgho brûlé, Hirsebrand*).

The disease was first described in Italy by Palmeri and Comes,[1] who have attributed it to the development of Saccharomycetes and bacteria. Later, in America, Burrill (1887) studied anew the blight, and, after having isolated sporogenous bacteria from the infected tissues, he attempted the inoculation of healthy plants. The results were variable; however, the author inferred the parasitism of the *Bacillus Sorghi*, nov. spec., and prescribed some measures for the preservation of plantations from the invasion of the disease. Analogous experiments by Kellerman and Swingle[2], more convincing than the preceding, because of the number of infections obtained, led to the same conclusions. More recently, Bruyning[3] has examined some plants of sorghum attacked by the blight, and formulated some conclusions different from those of the preceding authors. After having isolated several bacteria from the red tissues Bruyning retained two species which he considered the only factors of the fermentative disease, but these species are chromogenous outside the sorghum. These microbes acted symbiotically, superposing their respective pigments, the one yellow, the other red, the mixture giving the coloration observed in the tissues. These views were not supported by any experiment of inoculation.

I have recently studied some specimens of blighted sorghum coming from Algeria.[4] I was able to convince myself that in this case the phenomena of the blight were caused by the parasitic development of yeasts in the tissues of the plant.

[1] Notizie preliminari sopra alcuni fenomeni di fermentazione del Sorgo saccarino vivente (Accad. d. Sc. fis. e mat. di Napoli, fasc. 12, 1883).

[2] Report of Bot. Depart. of the Kansas Stat. Agri. Coll. 1888.

[3] La brûlure du Sorgho, etc., et les bactéries qui la provoquent (Arch. Néerland. 4e et 5e livr., pp. 297–330. 1898).

[4] These infected stems were sent to the botanical laboratory of the School of Pharmacy by Professor Trabut. Professor Guignard had the kindness to entrust me with the examination of them.

Already, by microscopic examination, it had been ascertained that in many regions of the central parenchyma of the stem the cells and the intercellular spaces enclosed masses of a small ovoid yeast, measuring from 1.5 to 2.5μ on an average. It was, moreover, the only microorganism which could be directly observed, even with great magnification and with the aid of staining reagents.

It was easy to isolate this yeast in a pure state by taking up the germs with a sterilized needle from the center of the stem, the section being made with a flamed scalpel, or by removing small cylinders of the red tissue from the pith by means of a sterilized trocar. The first culture liquid was a 5 per cent. glucose bouillon. Some subsequent isolations by means of Petri dishes with bouillon sugar gelatin have given, to the exclusion of all other organisms, white colonies formed by a yeast morphologically identical with that which had been observed in the diseased sorghum.

Cultivated on the surface of carrot, potato, and on different gelatin or gelose media with sugar, the yeast grows slowly in creamy-white colonies. It apparently keeps the same dimensions as those observed in the tissues of the plant. Sown in unfermented grape juice, or in various artificially sweetened liquids suitable for the culture of yeast, this organism shows a feeble alcoholic fermentation. The fermenting power is slightly increased by a series of re-sowings in the same medium. My attempts to obtain ascospores have been fruitless, and I am not able at present to classify this yeast with the true Saccharomyces.

The mere fact of isolating a yeast from the tissues of the blighted sorghum is not sufficient to enable one to conclude that this yeast is a parasite, and that it brings about the symptoms of the disease. It is known, in fact, that a large number of these ferments may be encountered on the surface of stems and leaves; it would not be astonishing, therefore, if some dead tissues, still containing in their cells a part of their reserve sugar, were invaded by the saprophytic development of a superficial yeast. The following experiments, however, show that the yeast isolated from the diseased sorghum does develop in the healthy tissues of the plant, and in them brings about the phenomena of the blight.

Sorghum plants raised from seed and cultivated in a hothouse during the months of November and December 1898 and January 1899 were inoculated with pure cultures. All aseptic precautions were

taken to avoid the introduction of foreign microbes. I used Dr. Roux's sterilizable syringe with a fine injection needle, in order to reduce to the minimum the wound necessary for the introduction of the culture. Only the stems were inoculated. The epidermis was exposed by cutting a small flap in the leaf sheath, carefully disinfecting by means of a red-hot iron, and, after the inoculation, the opening sealed by means of warm wax or sterilized paper. The plants experimented upon were successively examined at intervals of time varying from five days to two months. In every case the yeast had developed and multiplied in the intercellular spaces, and in the interior of the living cells to a distance of 10 to 15^{mm} above and below the point of inoculation.

The microscopical appearance was that which may be observed in the tissues of sorghum spontaneously infected; the lesion was also rendered visible in the same way by the red coloration of the parenchyma and fibrovascular bundles. These latter transfuse the coloring matter the whole length of the internode, and quite beyond the infected region, so that the appearance of the pigment at a certain point of the tissue is not a sure sign that the parasite is present at that point. On the surface of the stem may be observed long red lines corresponding to the outer bundles and their contiguous parenchyma seen through the transparent stem.

In these experiments, the isolation of the parasite from the affected pith has shown, by comparison with the control, that the parasitic yeast was the same as that in the cultures used as a starting point.

It is probable that the reserve sugars of the cells of the sorghum constitute the principal food of the parasite. Unfortunately the volume of infected tissue, limited and especially difficult to separate out, has not permitted the changes carried on by the parasite in the chemical composition of the plant to be estimated in this particular.

Are other yeasts capable of producing in the sorghum similar phenomena of parasitism? The following experiments answer in the affirmative. Inoculations have been made aseptically in the stems of healthy sorghum with pure cultures of wine yeast (round yeast of champagne [Bowzy]). The parasitism has been established under the same conditions as before, the yeast developing in the intercellular spaces and in the pith cells of the stem with the accompanying production of the characteristic red pigment, and with transfusion by the bundles of the internode.

On the other hand, what is the origin of the pigment? It is a general observation that wounds inflicted on the tissues of the sorghum developed a red coloration around the injured part. It is important to understand precisely in the preceding experiments the rôle of the local lesion induced by the inoculating needle. Aseptic punctures in the pith of healthy sorghum stems were made under conditions identical with those of the preceding experiments, the inoculating fluid alone being omitted. Under these conditions the pigment appeared in the wounded cells, but it was not abundant and was rigorously confined to the wound. The quantity of coloring matter thus produced is not capable of being carried by the bundles and of spreading beyond the actual point of the lesion. The experiment shows, however, that the chromogenous property belongs to the wounded cells of the sorghum.

From the preceding facts it may be concluded:

1. That yeasts may develop in the living cells of the sorghum.

2. That the parasitism of these yeasts may bring about an intense red coloration of the plant tissues, this coloration being the same as that which may be observed in the disease of sorghum called the *blight*. The production of the pigment appertains to the affected cells, and the parasite takes part only through the lesion which it produces.

These results confirm the old hypothesis of Palmeri and Comes, who, observing the fermentative phenomena of the red juice of the pith of the blighted sorghum, had inferred from it the parasitic action of the Saccharomycetes without giving it experimental proof. The same facts, moreover, are not contradictory of the experiments of Burrill, Kellerman, and Swingle. In fact, it may be concluded that, the red coloration being the result of a chromogenous function characteristic of the wounded cells of the plant, different parasites, yeasts or bacteria, may, by developing in the tissues, induce by continued lesion the production of a considerable quantity of the pigment.

On the contrary, it is necessary to make complete reservations as to the conclusions of Bruyning, who, attributing to the bacteria themselves the chromogenous function, denies to all micro-organisms lacking this function while outside the host plant the power of inducing the phenomena of sorghum blight.—MAXIME RADAIS, *School of Pharmacy, Paris.*

ROOT SUCKERS ON DOUGLAS FIR.

THE occurrence of stool shoots among deciduous species of trees is very common, and their production by the forester is resorted to for the reproduction of many species. Among conifers the formation of stool shoots is limited to a few species. The California redwood (*Sequoia sempervirens*) is very commonly reproduced in this way. Much less common than stool shoots are root shoots, often known as root suckers or suckers. Among conifers only the redwood, the California nutmeg (*Tumion Californica*), and the short-leaf or yellow pine (*Pinus echinata* Miller) have so far been reported as producing root suckers.

For several years the woodsmen of western Washington have recognized in the fir forests a curious growth which they have called "sap suckers." As we see them in the forest they appear as a broken stub ranging in height from 0.6 to 3.5^{m}. Without leaves or branches, they appear entirely lifeless until cut into with an axe. An examination shows that they are covered with living bark and beneath that a living woody tissue very hard and with a grain of very fine and intricate burl.

The sap suckers vary greatly in size and external appearance. The diameters range from 30 to 60^{cm} and the height from 0.6 to 3.5^{m}. Investigation has shown that they are connected with one of the main roots of the parent fir, their distance from the parent trunk varying from 0.6 to 4.5^{m}, an average distance being about 1.8^{m}. The living bark bears little resemblance to the bark of the fir except in color. The clefts are much finer and the plates much smaller. The living wood, in every instance, forms only an enveloping sheath about a decaying stub. It varies in thickness from 12 to 50^{mm} and there is great diversity in the disposition of this living sheath. It begins at or below the surface of the ground and grows upward, entirely encircling the decaying core. In many cases where the stub was very short the wood burl entirely covered it over, forming sometimes a low globular protuberance about 0.6^{m} high and sometimes a column 3.5^{m} high; but in the great majority of cases the burl covering has extended to only a portion of the height of the stub, so that the rotting dead end still protrudes above.

The "sap sucker" is only a secondary growth on an ordinary root sucker. The formation of these on the roots of the Douglas fir, *Pseudotsuga taxifolia*, was proven by examination. In the dense woods of

this region it is hard to distinguish the suckers from ordinary seedlings. Like most seedlings, those of the fir are very weak, and when they reach a maximum diameter of about 25^{cm} they die and begin to decay. At this time the formation of the secondary burl covering begins. The nourishment before given the sucker is utilized in covering over the dead and decaying stub with this new live growth.

In one instance a dead sucker had been covered with a primary burl covering to a height of 1.5^{m}. This had died, the bark had fallen off, and a second burl covering, still alive, had covered this over to a height of 0.9^{m}.

These suckers are found only in the moistest and densest forests. Even under the proper conditions they are very rare. They were observed in the summer of 1898, ten to fifteen miles from tide water, Chehalis county, Washington.— FRANK HAINES LAMB, *Biltmore, N. C.*

CURRENT LITERATURE.

BOOK REVIEWS.

General physiology.

THE RECEPTION by both European and American biologists of Verworn's *Allgemeine Physiologie* upon its publication late in 1895 was very cordial. The book awakened so widespread an interest that within three years a second edition was issued. This second edition has now been translated and edited by Dr. Frederic S. Lee, of Columbia University.[1] In its English dress the book will doubtless commend itself still further to English readers. Certainly it will put within reach of general readers a work that will give a better idea of the scope of physiology, and one that will present to special students readable and stimulating discussions of physiological problems.

The work may be called a treatise upon "general" physiology only in the peculiar sense that it discusses the general as opposed to the special functions of the cell. It does not deal with the functions of organs at all. On the whole the phrase *general cell physiology* would seem to describe it better.

It is a pleasure to find an animal physiologist who is yet to a reasonable degree familiar with plant physiology. But it is not for the views of plant function nor even for the facts adduced that the book may be commended to botanists. In these fields, indeed, one feels that Professor Verworn is traversing rather unfamiliar ground, in which he sometimes loses his way, to the leading astray of the unwary. Nevertheless the ability and suggestiveness of the book make it one which botanists inclined at all to physiology will do well to read. Professor Verworn has a luminous way of saying things, and while what he says sometimes suggests what not to say, more often his apt applications indicate others which he has not expressed.

The subjects treated, after an interesting introductory chapter on the aims and methods of physiological research, are as follows: living substance; its composition and the differences between living and lifeless substances; elementary vital phenomena, namely the phenomena of metabolism, of the changes of form, and of the transformation of energy; the general conditions

[1] VERWORN, MAX.—General physiology, an outline of the science of life. Translated from the second German edition and edited by FREDERIC S. LEE. 8vo. pp. xvi + 615. *figs. 285*. London and New York: The Macmillan Company. $4.00.

of life, including a discussion of the origin of life and the history of death; stimuli and their actions; and the mechanism of life.

No detailed discussion of the book need be entered upon, since it is already fairly well known in the original form. The translation has been admirably done by Professor Lee. The smooth and readable German of Verworn has been converted into easy and idiomatic English.—C. R. B.

Some popular books.

ALICE LOUNSBERRY is the author of *A guide to the wild flowers*[2] recently published. Mrs. Ellis Bowan has had charge of the illustrations, which consist of sixty-four colored and one hundred black and white plates, and fifty-four diagrams. Dr. N. L. Britton has written a brief introduction. The numerous attempts to provide easy and interesting ways of recognizing plants indicate a real demand and one that is very hopeful. Nature study is finding a prominent place in the schools, and any book which stimulates it properly is to be commended. The plants selected for this book are well illustrated and fairly well described, and should be recognized easily by the intelligent observer. Although strictly taxonomic, the plants are presented in ecological groups; as for example, "plants growing in water," "plants growing in moist soil," "plants growing in dry soil," etc., etc.—J. M. C.

ANOTHER RECENT book intended to encourage Nature study is *Field, forest, and wayside flowers*,"[3] by Maud Going (E. M. Hardinge). It professes to be "untechnical studies for unlearned lovers of nature," and is a charming book. The author does not deal in the usual fairy tales, but evidently knows what things are and what they are for, so far as current knowledge goes. The titles of the chapters are suggestive of the topical character of the book. A few of them are as follows: crocuses, dandelions, the flowering of the forest trees, green leaves at work, grasses, climbing plants, a handful of weeds, in winter woods, etc. The photographs are especially excellent, and some of our common plants are made to stand out with remarkable distinctness. The book can be commended to all those who wish to come into contact with nature in an untechnical way, and also to teachers in charge of nature study.—J. M. C.

EDWARD KNOBEL has attempted to make the identification of the grasses, sedges, and rushes of the northern United States an easy matter.[4] The plates

[2] A guide to the wild flowers. 8vo. pp. xvii + 347. New York: Frederick A. Stokes Company. 1899.

[3] Field, forest, and wayside flowers. 8vo. pp. xvi + 411. New York: The Baker & Taylor Company. 1899. $1.50.

[4] The grasses, sedges, and rushes of the northern U. S. 8vo. pp. 78. *pl.* 28. Boston: Bradlee Whidden. 1899. $1.00.

are numerous, and one of the features of the book is the series of marginal illustrations of essential structures opposite each description. Just how easy this will make the determination of species in these perplexing groups can be known only after experience. It is a question whether anything in clearness has been gained by substituting ear and earlet for spike and spikelet.—J. M. C.

A NEW NATURE READER has been provided by Kate Louise Brown, under the title *The plant baby and its friends*.[5] While the title suggests that the author has concerned herself with plant seedlings, a reading shows that the adult plant has received most consideration. Facts concerning many common plants are presented in the form of stories intended to be used as supplementary matter with younger children; and for such purpose the book should find a place. Some objectionable features of many books intended to assist children in nature study are happily absent from this book. Among these may be mentioned the treatment of fertilization and nomenclature. The stories concerning pollination are told in such an interesting way that even the youngest pupils should be interested. In some cases attempts at coloring as well as attempts at drawing lessons in morals from the plants studied have done violence to the facts, and the unfounded story of Egyptian mummy wheat is told once more. But aside from a few such errors it should be said that the plan and spirit of the book will make it very helpful with younger pupils.—OTIS W. CALDWELL.

FREDERICK LEROY SARGENT has produced an interesting little book for young people entitled *The corn plants, their uses and ways of life*.[6] Of course the phrase "corn plants" means cereals. The first pages are devoted to the mythology of the cereals, embracing the stories of classical antiquity to which allusions are so frequent in more modern literature.

For the botanist the chief interest is found in those pages which discuss the ecological adaptations of these important plants. A great deal of attention is given to such questions as protection against wind, weight, and excesses of moisture and dryness, several new drawings illustrating the structures which assist the plants in these respects. Few plants seem to be more interesting from the ecological standpoint, when one considers that they are grown in exposed places, absolutely unassisted by close relation with other plants which might serve to modify the effect of the wind or the sunlight.

In the section on the advantages of cereals as food-plants the author gives interesting descriptions of the methods of using cereals and the extent

[5] The plant baby and its friends. 8vo. pp. 155. Boston: Silver, Burdett & Company. 1899. 48 cents.

[6] The corn plants, their uses and ways of life. 8vo. pp. v + 106. *figs. 32.* Boston: Houghton, Mifflin & Company. 1899. 75 cents.

and geographical distribution of the various sorts. The book is full of good information put in an attractive style and should find abundant welcome.—O. W. CALDWELL.

MINOR NOTICES.

THE THIRD FASCICLE of "Illustrations de la Flore du Congo," by Wildeman and Durand, has just appeared, containing twelve plates, with descriptive text. The plates are exceedingly handsome, and their number has now reached thirty-six.—J. M. C.

A NEW classification of the Leucobryaceæ is proposed by M. Jules Cardot in *Revue Bryologique* **26**: 1–8. *pl. 1.* 1899. It is based chiefly upon the anatomical characters of the leaves as shown by cross-sections, such as the presence or absence of sclereides, and the form and arrangement of the chlorophyllose cells.—C. R. B.

SOME RESEARCHES of Loeb upon the influence of alkalies and acids upon embryonal development and growth[7] led to results which may have important applications to the growth of plants. He finds that weak alkalies (even .006% NaHO) accelerate the development and growth of larvæ of Arbacia (a sea-urchin) and the embryos of Fundulus (a fish), while weak acids retard. The cause of these actions is to be sought in the effect of the reagents on the oxidative processes of the protoplasm.—C. R. B.

NOTES FOR STUDENTS.

GEORGE J. PEIRCE has been studying the nature of the association of alga and fungus in lichens.[8] Speaking of the algæ he says that "it is neither logical nor sensible to conclude that their unusual position is beneficial to them," as free algæ can thrive, at least for a time, wherever lichens can. "There is no proof that algal cells serving as lichen gonidia are any better off as to food, protection, or situation than the average free algal cells of the same species." Of course the fungus is found to be absolutely dependent upon the alga. The author also affirms that the central body of the gonidial cells of Ramalina, Usnea, and Sphærophorus, is a nucleus, not a pyrenoid.—J. M. C.

HERMANN VON SCHRENK[9] has been investigating a disease of *Taxodium* known as peckiness, and also a similar disease of *Libocedrus decurrens*. In both cases the wood is destroyed in localized areas, which are surrounded by

[7] Archiv f. Entw.-mechanik der Organismen **7**: 631–641. *pl. 1.* 1898.

[8] Proc. Calif. Acad. Sci. III. **1**: 207–240. *pls. 41.* 1899.

[9] Eleventh Ann. Rep. Mo. Bot. Gard. 1–55. *pls. 6.* 1899.

wood apparently sound. In both, also, a fungus mycelium was found, which flourishes within the diseased centers, but no characters appeared by which it could be determined. It is interesting to note the fact that these two trees, similarly affected, are the representatives of a race largely extinct, and grow in different parts of the country.

The same author (*op. cit.* 6–70) has also discovered a peculiar sclerotioid disease of beech roots. Small tubercles were found attached to the fibrous roots, and upon examination these were found to be a twisted and contorted mass of rootlets invested by a sheath. It was impossible to determine the fungus, but it seemed probable to the author that it is distinct from those forming the mycorhiza.—J. M. C.

MESSRS. FARMER and WILLIAMS have continued their contributions to the life-history and cytology of the Fucaceæ by publishing a second paper[10] which deals with the development of the oogonia and oospheres, the phenomena of fertilization, and the early segmentation stages of the oospore, especially in the genera Fucus, Ascophyllum, and Pelvetia. The more interesting subjects discussed are the reduction in the number of chromosomes, the appearance and behavior of centrospheres and centrosomes, the formation of the walls of the oogonia, oospheres, and germinating oospore, and the part played by mucilage in bringing about the extrusion of the oospheres.

The reduction of chromosomes occurs in the papilla which is cut off to form the rudiment of an oogonium. This was also shown by Strasburger to be the case in Fucus. In the three successive mitoses by which the eight oosphere nuclei are formed, the reduced number of chromosomes is retained. Prominent centrospheres in the form of converging cytoplasmic radiations are present in every mitosis, whether of the oogonium or segmenting oospore. These could not be traced back to preexisting centrospheres, but appeared to arise independently by the activity of the protoplasm, and to disappear again after the mitosis. Though the centrospheres are cytoplasmic, the spindle between them is intranuclear in origin. Centrosome-like structures were sometimes seen within the centrospheres, but their number was not constant. There was no indication that the centrospheres of the first oosporic division are derived from the spermatozoid.

So few cases of polyspermy were observed that it is certain but one spermatozoid normally enters an oosphere. The existence of a wall around the newly fertilized eggs was conclusively demonstrated; such eggs burst when transferred from salt water to fresh, whereas unfertilized eggs similarly treated merely swell up but do not burst.

Some interesting features with regard to fertilization were observed in Halidrys. Groups of gyrating spermatozoids were seen distributed over the

[10] Phil. Trans. Roy. Soc., London, B. **190**: 623–645. 1898.

surfaces of the oospheres, each attached by one cilium. Suddenly the spermatozoids leave the egg "like a crowd of startled birds," the egg at the same time becoming covered with conical projections. The authors consider this phenomenon as marking the moment of fertilization, and as a proof of a definite repulsion of the supernumerary spermatozoids.—WILSON R. SMITH.

ALTHOUGH the morphology of the embryo sac is still a very live subject, it is well to study its physiological relations, as has been done by Mlle. Goldflus in the ovules of a large number of Compositae. She discusses especially the function of the antipodal cells and of the so-called epithelial layer.[11]

It is well known that, after the rupture of the nucellus, the embryo sac in this family lies in contact with the epidermis of the inner portion of the ovule. The cells of this layer frequently become enlarged and beautifully columnar, and for this reason Hegelmaier called the layer the "endodermis," ascribing to it a protective function. Schwere, without committing himself in regard to its function, changed the name to "endothelium." The author revives the term "epithelium," previously used by Warming and Goebel, assigning to the layer a digestive function, as did Guignard.

The antipodal cells, variable, as usual, both in number and size, are said to be digestive in some plants, and in others, conductive in function. Their densely staining protoplasm and their tendency to burrow back into the "pseudo-chalazal" region are cited in support of this view. Moreover, the cells of the inner part of the integument are arranged in rows converging from all sides toward the sac, this structure being well adapted for the conduction of nutriment to the embryo sac and its embryo.

The author has evidently fallen into the error of supposing that, because the *function* of the antipodal cells is now discovered, the view of Strasburger and others regarding their *homology* is no longer tenable. One would naturally expect a prothallial region of a gametophyte to nourish the reproductive region, even to digesting the food if necessary. Hence the two theories, instead of being mutually hostile, are in perfect harmony. Would the author say that the "epithelial layer" is not epidermis, merely because it has here a special function, that of digestion?

In reviewing the article by Chamberlain on *Aster Novae-Angliae*, the author rightly challenges an unguarded suggestion about a "macrospore in an unusual position," but closer reading would have shown that he was merely comparing the free nuclear division in the large antipodal cell with the same process in a macrospore; and it would also have become evident that he was not confounding the two terms "oosphere" and "macrospore."

[11] GOLDFLUS, MLLE. MATHILDE: Sur la structure et les fonctions de l'assise épithéliale et des antipodes chez les Composées. Journ. de Botanique **12**: 374–384. 1898; **13**: 9–17, 49–59, 87–96. 1899.

We cannot help wishing that the author had given complete drawings of some of the more striking ovules, such, for example, as *Dahlia gracilis*, with the cell contents accurately shown. When a point is proven "by the appearance of the protoplasm, and the distribution of starch and other foods in the ovule," one quite naturally expects in the drawings definite delineation. In this, however, the six plates are sadly lacking.

The author has touched an important and suggestive field. Results from a comparative study of other groups ought to be easily accumulated from the many permanent preparations of ovules and embryo sacs in the possession of various botanists, which might repay reexamination from this new point of view.— W. D. MERRELL.

NEWS.

DR. M. TREUB, director of the botanical gardens at Buitenzorg, has been elected a member of the Royal Society of London.

MR. H. G. TIMBERLAKE, instructor in botany in the University of Michigan, has accepted a corresponding position in the University of Wisconsin.

A BIOGRAPHICAL SKETCH, with portrait, of the late Edward Lewis Sturtevant is published by C. S. Plumb in the tenth report of the Missouri Botanical Garden.

MR. ERNST A. BESSEY has been appointed assistant in the Division of Vegetable Physiology and Pathology of the United States Department of Agriculture.

M. ED. PRILLIEUX, the eminent French phytopathologist, has been elected a member of the French Academy of Sciences, in the room of the late Charles Naudin.

PROFESSOR W. A. SETCHELL and other botanists of the University of California are about to leave on an expedition to study the flora of the Aleutian islands.—*Science*, June 23.

PROFESSOR P. H. ROLFS has been appointed professor of botany at Clemson College and botanist to the Agricultural Experiment Station of South Carolina, to succeed Dr. A. P. Anderson.

PROFESSOR HENRY G. JESUP, for twenty-two years professor of botany in Dartmouth College, Hanover, N. H., has resigned, and Mr. G. T. Moore, of Harvard University, has been appointed instructor in botany.

THE PROPRIETORS of *Nature* announce that they are about to reissue Sowerby's *English Botany*, third edition with supplement, containing descriptions and life size figures of every British plant, hand colored. The price varies from 16 to 19 guineas, according to binding.

THE INSTRUCTORS and fellows of the University of Chicago who have received botanical appointments for the coming year are as follows: Dr. O. W. Caldwell, professor of botany, State Normal School, Charleston, Ill.; John G. Coulter, assistant in charge of botany, Syracuse University; Florence May Lyon, assistant in botany, Smith College; Dr. W. D. Merrell, instructor in

charge of botany, University of Rochester; Herbert F. Roberts, assistant in Shaw School of Botany; Dr. Wilson R. Smith, instructor in charge of botany, McMaster University, Toronto, Canada.

THE BOTANICAL SEMINAR of the University of Nebraska is pushing work on the survey of the state and hopes to send additional parts of the "Flora" to the printer before the year is over. The Regents of the University made a small grant for a printing fund for the survey at their last meeting.

BY THE WILL of the late Professor O. C. Marsh, Yale University is given his fine residence with the extensive grounds and greenhouses for a botanic garden. The house may be used as the residence of the director, or as a botanical laboratory. It is to be hoped that this gift will stimulate Yale to develop its botanical work more worthily.

DR. EDWARD A. BURT, through the courtesy of Dr. W. G. Farlow, has been studying the Thelephoraceæ of the Curtis herbarium and published exsiccati in the cryptogamic herbarium at Harvard University. He expects to examine types and authentic specimens at Kew during July, spending the remainder of the summer in Sweden collecting and studying fleshy fungi.

AT CORNELL UNIVERSITY: Mr. W. A. Murrill has been appointed for the year as assistant cryptogamic botanist to the Experiment Station, to take charge of the work of Dr. B. M. Duggar during his absence in Europe. Messrs. Heinrich Hasselbring, Judson F. Clark, and George J. Hastings have been appointed assistants in botany. Dr. K. M. Wiegand has been promoted to an instructorship in botany.

AT THE UNIVERSITY OF MICHIGAN: Professor V. M. Spalding, who has been in California during the year, has returned to the East and will resume his work next autumn. Professor F. C. Newcombe will spend the summer in Paris to study the scientific institutes of that city. Dr. J. B. Pollock will have charge of the botanical work in the University summer school. Dr. Julia W. Snow and Mr. Pond will do work for the U. S. Fish Commission at Put-in-Bay.

THE PLANS of the botanical staff of the University of Iowa for the summer are as follows: Professor B. Shimek will be engaged in special studies of forestry problems in Iowa, under direction of the U. S. Department of Agriculture; Mr. T. E. Savage will probably complete his studies of the Mosses and Hepaticæ of the state; Mr. P. C. Myers will complete a photographic record of the diatoms of Iowa, recent and fossil; and Professor T. H. Macbride will probably spend the summer in the Grand Cañon of the Colorado, studying the forest problems there for report to the United States Department of Agriculture, and incidentally picking up the fungi of the region.

THE RHODE ISLAND College of Agriculture and Mechanic Arts, with the cooperation of Hon. Thomas B. Stockwell, state commissioner of public schools, and Dr. Horace S. Tarbell, superintendent of schools in Providence, proposes to open a summer school for nature study at Kingston, R. I., from July 5 to 19, 1899. A general summer school is not contemplated, and the work offered by the various departments constitutes a single course dealing solely with local phenomena in their adaptability to the teaching of nature study. The distinctive feature will be the study of living nature rather than post-mortem biology. Plants will be studied in the field, supplemented by laboratory work when necessary to a clear understanding of the subject treated. No attempt will be made to determine species, but it is proposed to treat the following topics: relation of plants to each other, relation of plants to animals, adaptations for cross pollination, and adaptations for the distribution of seeds and fruits. There will be no entrance examination, and no special requirements for completion of the course.